SHOUT
SHARE
IT

QE
701
B8X
NH

Bulletins of American Paleontology

Begun in 1895

VOLUME 108, NUMBER 347 **NOVEMBER 2, 1995**

SMITHSONIAN
NOV 20 1995
LIBRARIES

Latest Ordovician to Earliest Silurian Colonial Corals of the East-Central United States

by

Graham A. Young
and
Robert J. Elias

Paleontological Research Institution
1259 Trumansburg Road
Ithaca, New York, 14850 U.S.A.

Celebrating 100 years
1895–1995

PALEONTOLOGICAL RESEARCH INSTITUTION

Officers

PRESIDENT	JOHN C. STEINMETZ
VICE-PRESIDENT	RICHARD E. PETIT
SECRETARY	HENRY W. THEISEN
TREASURER	PAMELA WAIT
DIRECTOR	WARREN D. ALLMON

Trustees

R. TUCKER ABBOTT (to 6/30/96)
BRUCE M. BELL (to 6/30/96)
CARLTON E. BRETT (to 6/30/98)
WILLIAM L. CREPET (to 6/30/97)
J. THOMAS DUTRO, JR. (to 6/30/96)
SHIRLEY K. EGAN (to 6/30/98)
ANTON J. EGNER (to 6/30/97)
M. G. HARASEWYCH (to 6/30/98)
HARRY G. LEE (to 6/30/97)
AMY R. MCCUNE (to 6/30/97)
SAMUEL T. PEES (to 6/30/98)
RICHARD E. PETIT (to 6/30/96)
EDWARD B. PICOU (to 6/30/98)
GARY ROSENBERG (to 6/30/96)
CONSTANCE M. SOJA (to 6/30/97)
JAMES E. SORAUF (to 6/30/97)
JOHN C. STEINMETZ (to 6/30/97)
SUSAN B. STEPHENS (to 6/30/96)
HENRY W. THEISEN (to 6/30/98)
MARY KANE TROCHIM (to 6/30/98)
PAMELA WAIT (to 6/30/96)
THOMAS C. WHITELEY (to 6/30/97)

Trustees Emeritus

HARRY A. LEFFINGWELL
ROBERT M. LINSLEY
RAYMOND VAN HOUTTE
WILLIAM P. S. VENTRESS

BULLETINS OF AMERICAN PALEONTOLOGY
and
PALAEONTOGRAPHICA AMERICANA

WARREN D. ALLMON	EDITOR

Reviewers for this issue

WILLIAM A. OLIVER
JAMES E. SORAUF

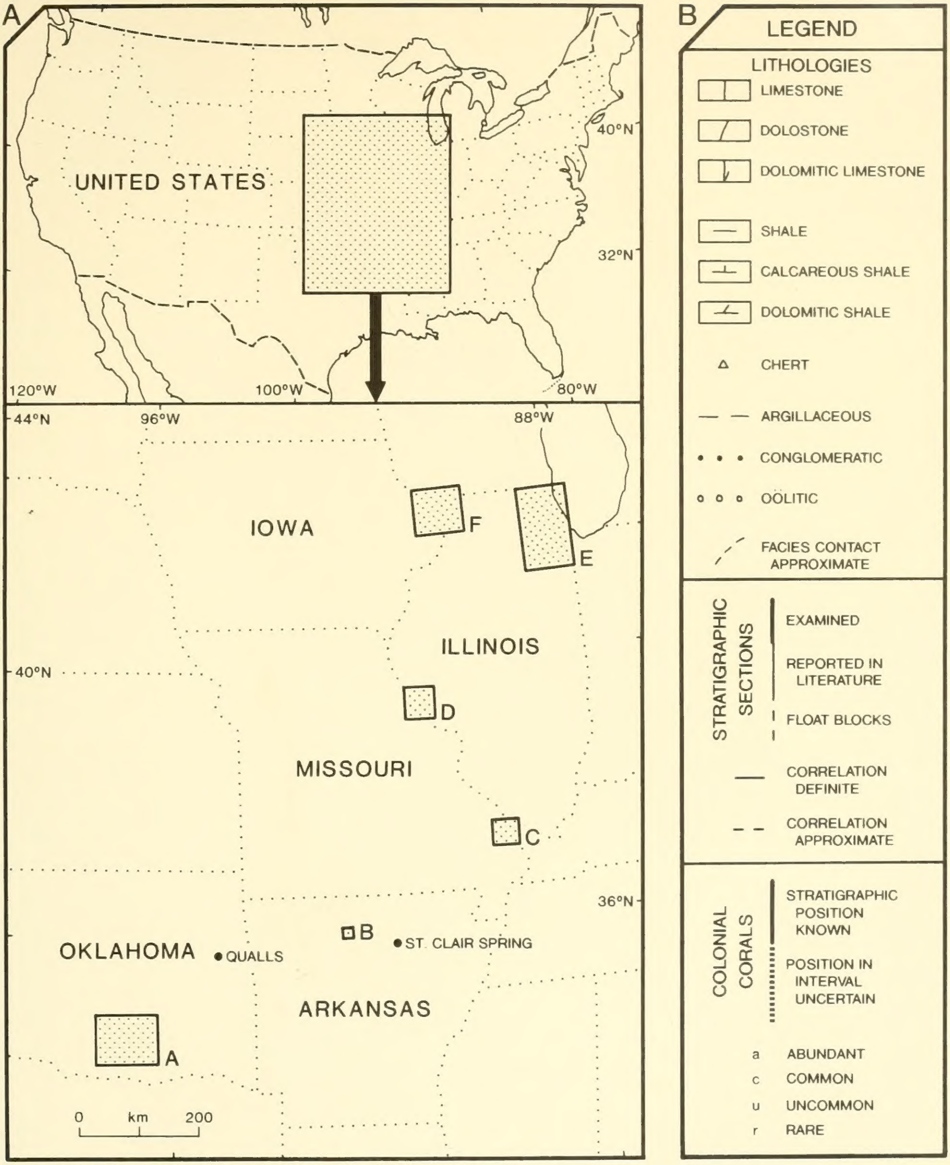
A list of titles in both series, and available numbers and volumes may be had on request. Volumes 1–23 of *Bulletins of American Paleontology* are available from Periodicals Service Company, 11 Main St., Germantown, New York 12526 USA. Volume 1 of *Palaeontographica Americana* has been reprinted by Johnson Reprint Corporation, 111 Fifth Ave., New York, NY 10003 USA.

Subscriptions to *Bulletins of American Paleontology* may be started at any time, by volume or year. Current price is US $62.50 per volume. Numbers of *Palaeontographica Americana* are priced individually, and are invoiced separately on request.

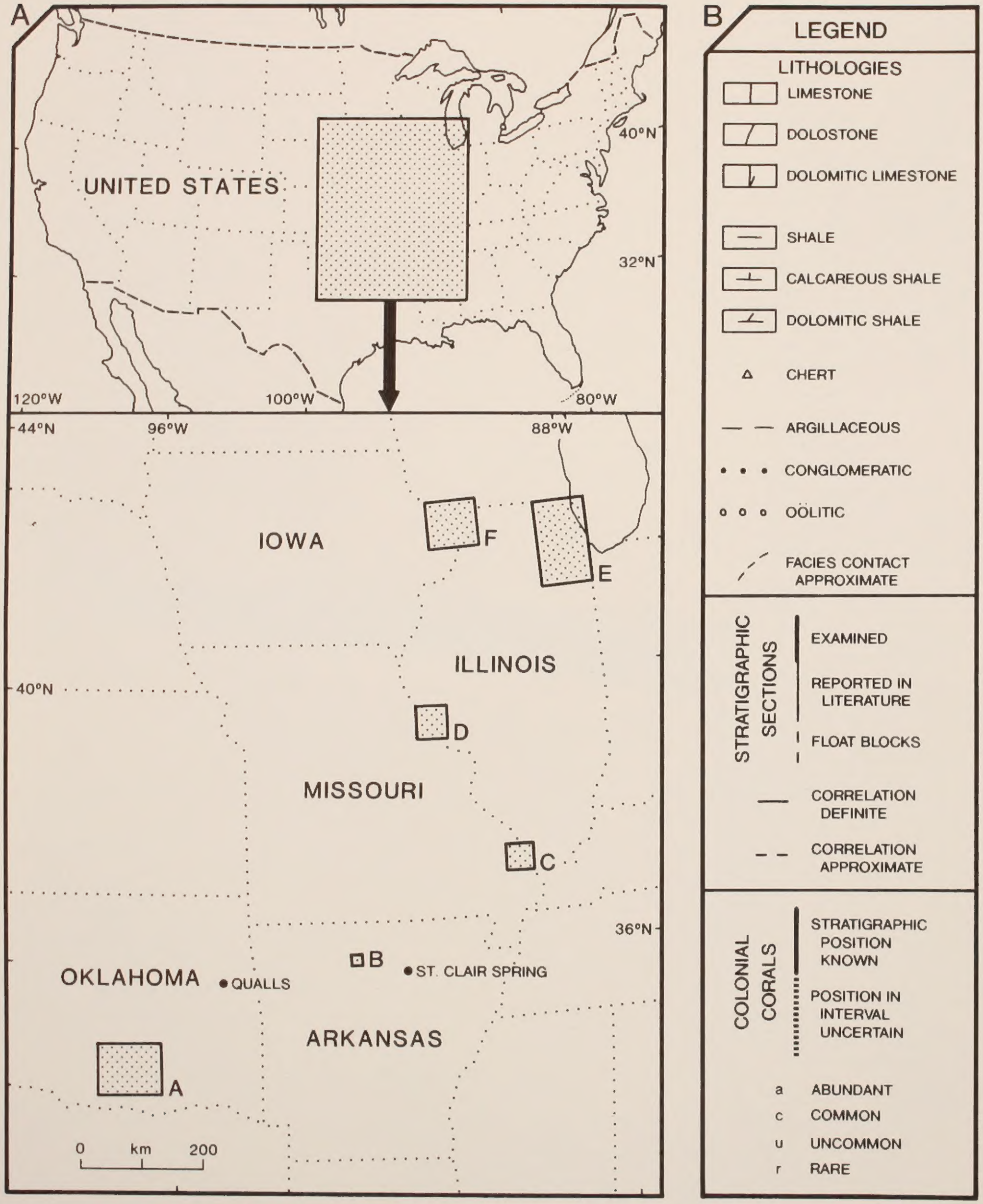
for additional information, write or call:

Paleontological Research Institution
1259 Trumansburg Road
Ithaca, NY 14850 USA
(607) 273-6623
FAX (607) 273-6620

∞ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).


A
UNITED STATES
40°N
32°N
120°W
100°W
80°W
44°N
96°W
88°W
IOWA
F
E
ILLINOIS
40°N
D
MISSOURI
C
36°N
B
OKLAHOMA
QUALLS
ST. CLAIR SPRING
ARKANSAS
A
0 km 200
B
LEGEND
LITHOLOGIES
LIMESTONE
DOLOSTONE
DOLOMITIC LIMESTONE
SHALE
CALCAREOUS SHALE
DOLOMITIC SHALE
CHERT
ARGILLACEOUS
CONGLOMERATIC
OOLITIC
FACIES CONTACT APPROXIMATE
STRATIGRAPHIC SECTIONS
EXAMINED
REPORTED IN LITERATURE
FLOAT BLOCKS
CORRELATION DEFINITE
CORRELATION APPROXIMATE
COLONIAL CORALS
STRATIGRAPHIC POSITION KNOWN
POSITION IN INTERVAL UNCERTAIN
a ABUNDANT
c COMMON
u UNCOMMON
r RARE

Text-figure 1.—**A**, Index map showing study region in the east-central United States, and detail map showing outcrop areas (A–F) of uppermost Ordovician and lowermost Silurian strata containing colonial corals of the Edgewood Assemblage within the Edgewood Province, and other localities mentioned in text. A = south-central Oklahoma, B = western north-central Arkansas, C = southern Illinois and southeastern Missouri, D = west-central Illinois and northeastern Missouri, E = northeastern Illinois, F = northwestern Illinois and eastern Iowa. Details of areas A–F are shown in Text-figures 2–7. **B**, Legend of symbols for Text-figures 2–7.


A
UNITED STATES
40°N
32°N
120°W
100°W
80°W
44°N
96°W
88°W
IOWA
F
E
ILLINOIS
40°N
D
MISSOURI
C
36°N
OKLAHOMA
QUALLS
B
ST. CLAIR SPRING
ARKANSAS
A
0 km 200
B
LEGEND
LITHOLOGIES
LIMESTONE
DOLOSTONE
DOLOMITIC LIMESTONE
SHALE
CALCAREOUS SHALE
DOLOMITIC SHALE
CHERT
ARGILLACEOUS
CONGLOMERATIC
OOLITIC
FACIES CONTACT APPROXIMATE
STRATIGRAPHIC SECTIONS
EXAMINED
REPORTED IN LITERATURE
FLOAT BLOCKS
CORRELATION DEFINITE
CORRELATION APPROXIMATE
COLONIAL CORALS
STRATIGRAPHIC POSITION KNOWN
POSITION IN INTERVAL UNCERTAIN
a ABUNDANT
c COMMON
u UNCOMMON
r RARE

Text-figure 1.—**A**, Index map showing study region in the east-central United States, and detail map showing outcrop areas (A–F) of uppermost Ordovician and lowermost Silurian strata containing colonial corals of the Edgewood Assemblage within the Edgewood Province, and other localities mentioned in text. A = south-central Oklahoma, B = western north-central Arkansas, C = southern Illinois and southeastern Missouri, D = west-central Illinois and northeastern Missouri, E = northeastern Illinois, F = northwestern Illinois and eastern Iowa. Details of areas A–F are shown in Text-figures 2–7. **B**, Legend of symbols for Text-figures 2–7.

PALEONTOLOGICAL RESEARCH INSTITUTION
FOUNDED 1932

Bulletins of American Paleontology

Begun in 1895

VOLUME 108, NUMBER 347 **NOVEMBER 2, 1995**

SMITHSONIAN
NOV 20 1995
LIBRARIES

Latest Ordovician to Earliest Silurian Colonial Corals of the East-Central United States

by

Graham A. Young
and
Robert J. Elias

Paleontological Research Institution
1259 Trumansburg Road
Ithaca, New York, 14850 U.S.A.

ISSN 0007-5779
ISBN 0-87710-438-7
Library of Congress Catalog Card Number: 95-71052

Printed in the United States of America
Allen Press, Inc.
Lawrence, KS 66044 U.S.A.

CONTENTS

Page
Abstract ... 7
Introduction ... 7
Acknowledgments ... 9
Distribution of Colonial Corals
  Introduction ... 9
  South-Central Oklahoma ... 9
  Western North-Central Arkansas ... 10
  Southern Illinois and Southeastern Missouri ... 10
  West-Central Illinois and Northeastern Missouri ... 13
  Northeastern Illinois ... 13
  Northwestern Illinois and Eastern Iowa ... 14
Colonial Coral Assemblages ... 14
Age of Units and Regional Correlation ... 14
Biogeography and Events
  Edgewood Province ... 19
  Silurian Assemblage ... 21
The Edgewood Colonial Corals: Taphonomy and Paleoecology
  Introduction ... 22
  Abrasion ... 22
  Orientation ... 23
  Composite Coralla ... 24
  Encrusting Relationships ... 25
  Borings ... 27
  Growth Form ... 27
  Growth Rate ... 31
  Corallum Size ... 32
  Paleoenvironments ... 33
Aspects of Intraspecific Variation
  Introduction ... 34
  Variation in Individual Species ... 35
  Comparisons of Species ... 40
Systematic Paleontology
  Introduction ... 42
  Biometric Methods ... 43
  Collectors and Repositories ... 44
  Systematics ... 44
    Class Anthozoa Ehrenberg, 1834
      Subclass Tabulata Milne-Edwards and Haime, 1850
        Order Heliolitida Frech, 1897 ... 44
          Family Proporidae Sokolov, 1949
            Genus *Propora* Milne-Edwards and Haime, 1849 ... 44
              Propora thebesensis (Foerste, 1909) ... 45
              Propora savagei n. sp. ... 56
              Propora speciosa (Billings, 1865) ... 58
              Propora sp. aff. *P. affinis* (Billings, 1865) ... 62
              Propora sp. A ... 63
          Family Plasmoporidae Sardeson, 1896
            Genus *Plasmopora* Milne-Edwards and Haime, 1849 ... 63
              Plasmopora sp. cf. *P. logani* Young and Noble, 1990b ... 64
          Family Coccoseridiae Kiaer, 1899
            Genus *Acidolites* Lang, Smith, and Thomas, 1940 ... 65
              Acidolites sp. A ... 65
            Genus *Protaraea* Milne-Edwards and Haime, 1851 ... 65
              Protaraea sp. A ... 66
        Order Halysitida Sokolov, 1947 ... 66
          Family Halysitidae Milne-Edwards and Haime, 1849
            Genus *Halysites* Fischer von Waldheim, 1828 ... 67
              Halysites alexandricus n. sp. ... 67
              Halysites sp. cf. *H. alexandricus* n. sp. ... 72
              Halysites? sp. A ... 73

Genus *Catenipora* Lamarck, 1816 ... 74
Catenipora lawrenciea n. sp. ... 74

Order Favositida Wedekind, 1937
Suborder Favositina Wedekind, 1937
Superfamily Favositicae Dana, 1846
Family Favositidae Dana, 1846

Subfamily Favositinae Dana, 1846 ... 77
Genus *Paleofavosites* Twenhofel, 1914 ... 77
Paleofavosites subelongus (Savage, 1913) ... 78
Paleofavosites sp. cf. *P. subelongus* (Savage, 1913) ... 89
Paleofavosites adaensis n. sp. ... 91
Paleofavosites sp. cf. *P. ivanovi* Sokolov, 1951a ... 94
Paleofavosites sp. A ... 96

Order Auloporida Sokolov, 1947
Superfamily Auloporicae Milne-Edwards and Haime, 1851
Family Auloporidae Milne-Edwards and Haime, 1851

Genus *Aulopora* Goldfuss, 1829 ... 97
Aulopora sp. A ... 97

Order Tetradiida Okulitch, 1936
Family Tetradiidae Nicholson, 1879

Genus *Rhabdotetradium* Sokolov, 1955 ... 99
Rhabdotetradium sp. A ... 99

Subclass Rugosa Milne-Edwards and Haime, 1850
Order Stauriida Verrill, 1865
Suborder Stauriina Verrill, 1865
Family Stauriidae Milne-Edwards and Haime, 1850

Genus *Palaeophyllum* Billings, 1858 ... 101
Palaeophyllum sp. ... 101

Family Pycnostylidae Stumm in Shrock and Twenhofel, 1953

Genus *Pycnostylus* Whiteaves, 1884 ... 102
Pycnostylus sp. A ... 102
Appendix: Stratigraphic Sections ... 104
References Cited ... 106
Plates ... 117
Index ... 139

LIST OF ILLUSTRATIONS

Text-figure Page
1. Index map showing study region in the east-central United States, and legend of symbols for Text-figures 2–7 ... foldout inside front cover
2. Locality map and stratigraphic sections in south-central Oklahoma ... 10
3. Locality map and stratigraphic section in western north-central Arkansas ... 10
4. Locality map and stratigraphic sections in southern Illinois and southeastern Missouri ... 11
5. Locality map and stratigraphic sections in west-central Illinois and northeastern Missouri ... 12
6. Locality map and stratigraphic sections in northeastern Illinois ... 15
7. Locality map and stratigraphic sections in northwestern Illinois and eastern Iowa ... 16
8. Composite stratigraphic sections showing uppermost Ordovician and lowermost Silurian units and distribution of colonial corals in the east-central United States ... foldout inside back cover
9. Biogeographic and paleogeographic features in eastern and central North America ... 20
10. Triangle diagrams showing growth forms of *Propora thebesensis* and *Paleofavosites subelongus* ... 28
11. Comparison of coefficients of variation for selected parameters in several species of Tabulata from the east-central United States ... 41
12. Transverse sections illustrating astogeny and corallite increase in *Propora thebesensis* ... 48
13. Tabularium size-frequency distributions for selected coralla of *Propora thebesensis* ... 50
14. Intercorallum variation in morphologic characters of *Propora thebesensis* from the east-central United States ... 51
15. Comparison of selected species of *Propora* ... 52
16. Serial transverse sections illustrating corallite increase in a corallum of *Propora savagei* ... 57
17. Intraspecific variation in *Propora savagei* ... 57
18. Relationship between mean tabularium area and mean corallite area in *Propora speciosa* (and probable synonyms) from several regions ... 60
19. Intraspecific variation in *Halysites alexandricus* ... 71

20. Relationship between mean tabularium width and mean tabularium length in halysitid species from the east-central United States 73
21. Serial transverse sections illustrating corallite increase in a corallum of *Catenipora lawrencica* 75
22. Serial transverse sections illustrating basal astogeny in a corallum of *Paleofavosites subelongus* 81
23. Serial transverse sections illustrating corallite increase in *Paleofavosites subelongus* 82
24. Frequency distributions of average corallite dimension and polygonality for selected coralla of *Paleofavosites subelongus* 84
25. Intercorallum variation in morphologic characters of *Paleofavosites subelongus*, Part 1 85
26. Intercorallum variation in morphologic characters of *Paleofavosites subelongus*, Part 2 86
27. Comparison of selected species of *Paleofavosites* 87
28. Frequency distributions of average corallite dimension and polygonality for two coralla of *Paleofavosites* sp. cf. *P. subelongus* ... 90
29. Frequency distributions of average corallite dimension and polygonality for two coralla of *Paleofavosites adaensis* 92
30. Frequency distributions of average corallite dimension and polygonality for one corallum of *Paleofavosites* sp. cf. *P. ivanovi* 95
31. Frequency distributions of average corallite dimension and polygonality for one corallum of *Paleofavosites* sp. A 96
32. Intraspecific variation in *Aulopora* sp. A 97
33. Relationship between number of major septa and corallite diameter in *Palaeophyllum* sp. 101
34. Intraspecific variation in *Pycnostylus* sp. A 103

LIST OF TABLES

Table Page
1. Colonial corals of the Edgewood Assemblage, relative abundance, and distribution in the east-central United States 17
2. Colonial corals of the Silurian assemblage in the study region, east-central United States 18
3. Conditions, orientations, and types of tabulate coralla in selected units within the Edgewood Province 23
4. Orientations of massive Edgewood tabulate coralla in various size and growth form categories 24
5. Encrusting relationships involving colonial corals in selected units within the Edgewood Province 26
6. Corallum growth forms of selected tabulate species in units within the Edgewood Province 29
7. Growth forms and spacing of tabulae and dissepiments in selected tabulate coralla from the Edgewood Province 30
8. Sizes of massive tabulate coralla in selected units within the Edgewood Province 33
9. Environmental interpretations for selected units within the Edgewood Province 36
10. Interlocality variation in qualitatively defined morphologic characters of *Propora thebesensis* in the east-central United States ... 38
11. Interlocality variation in quantitatively defined morphologic characters of *Propora thebesensis* in the east-central United States .. 38
12. Interlocality variation in qualitatively defined morphologic characters of *Paleofavosites subelongus* in the east-central United States 39
13. Interlocality variation in quantitatively defined morphologic characters of *Paleofavosites subelongus* in the east-central United States 40
14. Growth forms of coralla by species and collection intervals in the east-central United States 46
15. Biometric data for proporids from the east-central United States 47
16. Biometric data for one corallum of *Plasmopora* sp. cf. *P. logani* from the east-central United States 64
17. Biometric data for one corallum of *Protaraea* sp. A from the east-central United States 66
18. Biometric data for halysitids from the east-central United States 69
19. Biometric data for favositids from the east-central United States 79
20. Biometric data for *Aulopora* sp. A from the east-central United States 98
21. Biometric data for *Palaeophyllum* sp. from the east-central United States 101
22. Biometric data for *Pycnostylus* sp. A from the east-central United States 103

LATEST ORDOVICIAN TO EARLIEST SILURIAN COLONIAL CORALS OF THE EAST-CENTRAL UNITED STATES

GRAHAM A. YOUNG[1] AND ROBERT J. ELIAS

Department of Geological Sciences, The University of Manitoba,
Winnipeg, Manitoba R3T 2N2 CANADA

ABSTRACT

A distinctive assemblage of colonial corals occurs in uppermost Ordovician (Gamachian) to lowermost Silurian (lower Rhuddanian) strata within the east-central United States. This Edgewood Assemblage is strikingly different from Late Ordovician assemblages that preceded it in other parts of the North American cratonic interior, and differs from the Silurian assemblage that succeeded it. The Edgewood Assemblage existed during an important time of global environmental change and mass extinction. Some of the taxa have an Ordovician character; these include the youngest North American tetradiid, which is among the last representatives of an important Ordovician order. Other taxa represent first appearances of typically Silurian forms: the oldest definite plasmoporid, the earliest North American *Halysites,* and the first pycnostylid. Our study analyzes this significant assemblage in terms of biostratigraphy, biogeography, taphonomy, paleoecology, and intraspecific variability; the Silurian assemblage is also documented. With this information, we contribute to the knowledge of corals and the history of biological and physical events during this critical time interval, and to the solution of geologic problems such as the age, correlation, and depositional environment of stratigraphic units.

Colonial corals of the Edgewood Assemblage occur in Oklahoma, Arkansas, Missouri, and Illinois, occupying a region known as the Edgewood Province. We recognize the following new taxa: *Propora savagei* n. sp., *Halysites alexandricus* n. sp., and *Catenipora lawrencica* n. sp. Diversity in this province generally decreases northward, reflecting a gradient from the most open, normal-marine conditions nearest the paleocontinental margin, to increasing restriction farther into the interior. Detailed paleoenvironmental determinations are possible using comparative taphonomy and paleoecology. Proportions of abraded coralla and degrees of abrasion increase with energy level. Proportions of coralla in growth orientation are higher in lower energy environments; they also increase from columnar growth forms to bulbous and high domical forms to low domical forms, and with corallum size. Ratios of bulbous:domical forms and corallum height:width, and usually inferred growth rates, increase with sedimentation rate and decreasing substrate stability. Proportions of composite coralla increase with decreasing sediment cohesion and substrate stability. Large corallum sizes reflect prolonged environmental stability. In some cases, corals are active encrusters and substrates for encrusters; this indicates substrate availability and stability, low sedimentation rate, and low turbidity.

Two or perhaps three species of the Edgewood Assemblage occur outside the Edgewood Province. The strongest affinities of this assemblage are with latest Ordovician to earliest Silurian coral faunas of Anticosti Island, Québec. The Edgewood Assemblage is strikingly different from the slightly older, typical Late Ordovician faunas in the North American interior. The disappearance of these typical Ordovician assemblages was related to habitat loss during a major glacio-eustatic drop at the end of the Richmondian. In the Gamachian, minor transgressions into the southern–central portion of the Edgewood Province occurred as sea level fluctuated during the glacial maximum. Corals were introduced from the continental margin or were derived from forms previously restricted to the margin. Dispersion into the northern part of the province accompanied expansion of suitable habitat areas during the early phase of the major latest Gamachian–Rhuddanian transgression associated with deglaciation.

Colonial corals are uncommon in strata immediately above those containing the Edgewood Assemblage in the east-central United States. This Silurian assemblage, including *Paleofavosites adaensis* n. sp., appears in the upper Rhuddanian. The changeover from Edgewood to Silurian assemblages occurred as water depth and temperature were generally increasing during the Rhuddanian, but apparently coincided with a minor regressive event. We infer that as areas in the east-central United States became inhospitable, geographic ranges of Edgewood species were reduced. Most became extinct, but some underwent rapid evolution in small populations. The descendants dispersed and new immigrants arrived as suitable habitat areas expanded when the transgression resumed. Two Edgewood species survived briefly in a local refugium.

Comparisons of patterns of variation in different species indicate that inherent variabilities of different coral orders are not the same, and that certain types of variation tend to recur among species and among orders. Some of the general similarities and differences among taxa are linked principally to structural factors that controlled the ways in which colonial corals grew. Genotypic and ecophenotypic factors acted in concert with the structural control of growth to determine variation within individual species.

INTRODUCTION

The best known, most fossiliferous, and perhaps stratigraphically most complete Ordovician–Silurian boundary sections in the cratonic interior of North America occur in the east-central United States (see Bergström and Boucot, 1988; Text-fig. 1A, index map, foldout inside front cover). Upper Ordovician Richmondian beds were deposited in a vast epeiric sea and are mainly argillaceous. They are succeeded by uppermost Ordovician (Gamachian) to lowermost Silurian (lowermost Llandovery) units that are predominantly carbonate, typically thin, and of limited areal distribution. These in turn are overlain by carbonate strata of Llandovery age. The Gamachian beds represent a regressive phase corresponding to the latest Ordovician glacial maximum, but were probably deposited during minor transgressions as sea level fluctuated (see Amsden, 1986; McAuley and Elias, 1990). Lower Llandovery sediment accumulated during the major transgression associated with deglaciation. During Late Ordovician to Early Silurian time, North America was located on the equator, unattached to other paleocontinents (Scotese and McKerrow, 1990, figs. 9, 10). Continental glaciation in the latest Ordovician was centered on the African portion of Gondwana, in a south-polar position (Brenchley *et al.,* 1991, fig. 1).

---

[1] Present address: Manitoba Museum of Man and Nature, 190 Rupert Avenue, Winnipeg, Manitoba R3B 0N2, CANADA.

The biotas within these deposits in the east-central United States are of particular importance for several reasons. Stratigraphic and geographic distributions of various groups must be determined in order to establish a means for reliable age determination and correlation in regions where graptolites used to define the systemic boundary are absent (see Bergström and Boucot, 1988). The major mass extinction during latest Ordovician time may have been the second largest in the Phanerozoic (Sepkoski, 1986). This mass extinction and subsequent recovery in the Early Silurian have been related to global climatic, eustatic, and oceanographic changes (*e.g.,* Brenchley, 1989). In order to understand fully the patterns and processes of these bioevents, much remains to be learned at the species level in an accurate framework of time, environment, and biogeography. Data from cratonic interiors are essential because of the importance of "perched faunas" in the extensive epeiric seas that were characteristic of the Paleozoic (see Sheehan, 1988). Evolution and extinction in these faunal realms seem to have been related to the recurrent transgressions and regressions in cratonic areas. Faunal groups in the uppermost Ordovician to lowermost Silurian of the east-central United States that are best known are the brachiopods (*e.g.,* Amsden, 1974, 1986), conodonts (*e.g.,* Thompson and Satterfield, 1975; Barrick, 1986), and corals (see below).

The distinctive assemblage of solitary and colonial corals that occurs in Gamachian to lower Lower Llandovery (lower Rhuddanian) strata of the east-central United States has been termed the Edgewood Assemblage (see Elias and Young, 1992; Text-fig. 1A, detail map). The subclasses Rugosa Milne-Edwards and Haime and Tabulata Milne-Edwards and Haime are represented. The only coral known from the immediately underlying Richmondian beds in this region is *Salvadorea randi* (Elias), a solitary rugosan; it is not related to any Edgewood species. The Edgewood Assemblage is succeeded by an assemblage of Silurian rugose and tabulate corals in upper Lower Llandovery (upper Rhuddanian) strata. Our present comprehensive study of the Tabulata and colonial Rugosa in these deposits forms a companion to the work on solitary Rugosa by Elias (1982, 1992) and McAuley and Elias (1990). Together, these publications comprise the first thorough examination of an entire coral fauna from the latest Ordovician to earliest Silurian.

In this monograph we precisely document the full stratigraphic and geographic distribution of the Edgewood colonial corals, consider their biostratigraphic and biogeographic significance, and investigate their taphonomy, paleoecology, and intraspecific variability. Colonial corals of the succeeding Silurian assemblage in the study region are also documented because of their importance in delineating the stratigraphic limits of the Edgewood Assemblage and in interpreting the history of events, both biological and physical. With this information, we contribute to the knowledge of corals during this critical time interval, and to the solution of geologic problems such as the age, correlation, and depositional environment of units and the effects and timing of sea-level changes. Syntheses based on the entire solitary and colonial coral fauna in uppermost Ordovician to lowermost Silurian strata of the east-central United States have been and will be presented elsewhere (*e.g.,* Elias and Young, 1992).

Strata containing corals of the Edgewood Assemblage are exposed in six outcrop areas (Text-fig. 1A, detail map, foldout inside front cover). The region of the east-central United States in which this particular assemblage occurs has been named the Edgewood Province (Elias, 1982). We selected 32 stratigraphic sections for examination in this study. They provide representative geographic coverage of the interval containing Edgewood corals, as well as some exposure of the immediately underlying and overlying beds. All sections have been described in previous literature, and fossils have been listed from most (see *Appendix,* pp. 104–106). Each stratigraphic section, as well as a bulk rock sample provided by W. W. Craig from the section in north-central Arkansas, was thoroughly examined for colonial coralla. All specimens seen were collected; they were found at 24 sections. Additional material from some of these, as well as other sections, was incorporated into our study from collections made by R. J. Elias and R. J. McAuley in Oklahoma and southeastern Missouri, by A. F. Foerste in southern Illinois, by T. E. Savage in southern and northeastern Illinois and northeastern Missouri, and by H. F. Crooks in northeastern Illinois.

A total of 324 colonial coralla of the Edgewood Assemblage and 37 from the Silurian assemblage are identified to the species level and documented here. Their abundance within collection intervals in the stratigraphic sections we studied was estimated qualitatively, taking into account the absolute number of specimens, thickness and lateral extent of the interval, and quality of the exposure. Ranges in number of coralla for each abundance category are as follows: rare, 1–2; uncommon, 2–6; common, 4–19; and abundant, 11–50.

Colonial coralla from elsewhere in North America were examined for comparative purposes as necessary. We studied one specimen from the Hudson Bay Lowland of Manitoba, six from southern Ontario, six from the Gaspé Peninsula of Québec, and ten from Anticosti Island, Québec.

ACKNOWLEDGMENTS

This project and the Research Associateship of G. A. Young were funded by grants to R. J. Elias from the Natural Sciences and Engineering Research Council of Canada and The University of Manitoba, and by University of Manitoba Postdoctoral Fellowships held by G. A. Young. We were ably assisted by V. L. F. Young during field work in 1990. C. A. M. Duncan and R. G. Zeilstra (University of Manitoba) prepared most of the thin sections and many of the acetate peels.

We are grateful to W. W. Craig (University of New Orleans, New Orleans, Louisiana) for providing a bulk rock sample from Arkansas. We thank R. L. Langenheim, Jr. (University of Illinois at Urbana–Champaign, Urbana, Illinois) and J. Kluessendorf (Illinois State Geological Survey, Champaign, Illinois) for assistance in locating the T. E. Savage collections at the University of Illinois at Urbana–Champaign, and D. B. Blake (University of Illinois at Urbana–Champaign, Urbana, Illinois) for permitting the loan of specimens. T. E. Bolton (Geological Survey of Canada, Ottawa, Ontario), J. W. M. Thompson (National Museum of Natural History, Smithsonian Institution, Washington, D.C.), J. B. Waddington (Royal Ontario Museum, Toronto, Ontario), and R. D. White (Peabody Museum of Natural History, Yale University, New Haven, Connecticut) arranged loans of material from repositories in their charge. J. G. Carter (University of North Carolina, Chapel Hill, North Carolina) provided information regarding the collection of P. K. Birkhead.

We appreciate the helpful comments received from the reviewers, W. A. Oliver, Jr. (United States Geological Survey, Washington, D.C.) and J. E. Sorauf (Binghamton University, Binghamton, New York), and the editor, W. D. Allmon (Paleontological Research Institution, Ithaca, New York).

DISTRIBUTION OF COLONIAL CORALS

INTRODUCTION

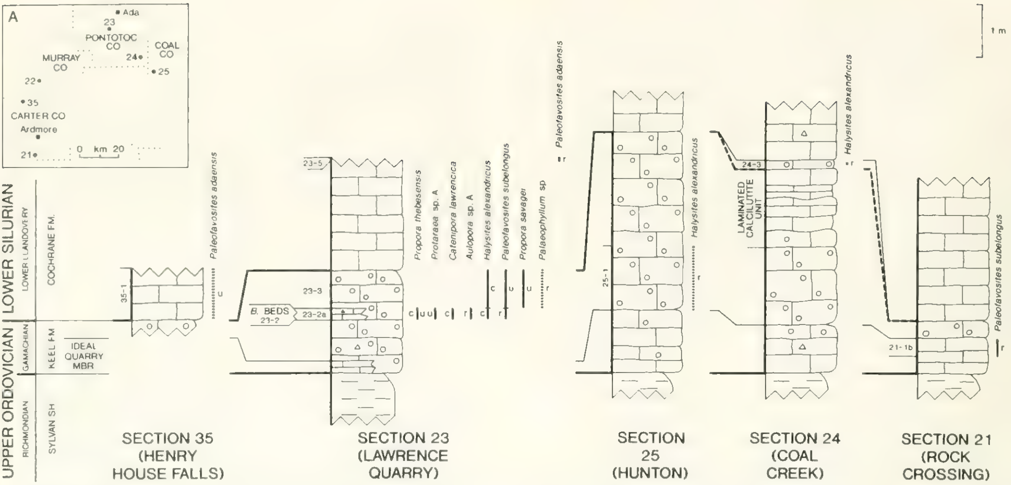
Uppermost Ordovician to lowermost Silurian deposits containing corals of the Edgewood Assemblage occur in six outcrop areas in the east-central United States (Text-fig. 1A, foldout inside front cover). McAuley and Elias (1990, pp. 9–23) discussed the lithostratigraphy, biota, age, and paleoenvironment for each area (see also Elias, 1992). The history of study and the distribution of colonial corals in these areas are documented below.

SOUTH-CENTRAL OKLAHOMA

Uppermost Ordovician to lowermost Silurian stratigraphy in this area is shown in Text-figure 2. Corals are not known to occur in the Sylvan Shale. Colonial corals identified as *Lyellia thebesensis* Foerste and *Halysites catenularia* (Linnaeus) were listed from the Ideal Quarry Member of the Keel Formation by Maxwell (1936, p. 49, table 1; unit referred to as Hawkins Limestone therein). The following have been reported previously from oölites of the Keel Formation: *Favosites niagarensis* Hall (Reeds, 1911, p. 259; upper oölitic zone, oölitic member, Chimneyhill Limestone therein); *L. thebesensis, H. catenularia, Favosites favosus* (Goldfuss), and *Favosites* sp. (Maxwell, 1936, table 2); and *Halysites* sp. (Amsden, 1957, p. 15; 1960, p. 44).

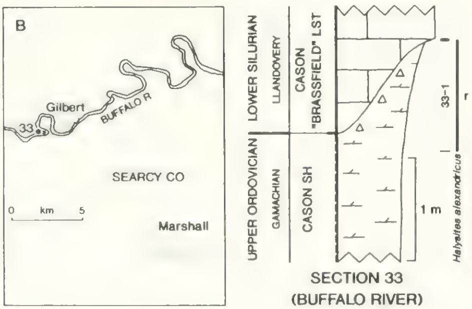
Paleofavosites subelongus (Savage) was the only species recovered from the Ideal Quarry Member of the Keel Formation during the present study. We found the following in the *Brevilamnulella* beds of the Keel: *Propora thebesensis* (Foerste), *Protaraea* sp. A, *Halysites alexandricus* n. sp., *Catenipora lawrencica* n. sp., *P. subelongus,* and *Aulopora* sp. A. The colonial rugose corals that McAuley and Elias (1990, p. 8) reported seeing in the *Brevilamnulella* beds may have been coralla of *P. subelongus* with prominent septal spines. From oölites in the lower Keel Formation (Section-intervals 23-2a, 23-3, 25-1), we obtained *P. thebesensis, Propora savagei* n. sp., *H. alexandricus, P. subelongus,* and *Palaeophyllum* sp. The only colonial coral we discovered in an oölite of the upper Keel (Section-interval 24-3) is *H. alexandricus.* Coralla were not observed in the Keel at Section 22 (Cedar Village).

From the Cochrane Formation, *Favosites favosus* was listed by Reeds (1911, table 2; glauconitic member, Chimneyhill Limestone therein), and that species as well as *Halysites catenularia* were identified by Maxwell (1936, p. 59, table 3). In the lower Cochrane, we found only *Paleofavosites adaensis* n. sp. The distribution of corals in the Keel and Cochrane formations, based on collections made during the present study, is shown in Text-figure 2.


A
Ada
23
PONTOTOC CO
COAL CO
MURRAY CO
24
25
22
35
CARTER CO
Ardmore
21
0 km 20
UPPER ORDOVICIAN
LOWER SILURIAN
RICHMONDIAN
GAMACHIAN
LOWER LLANDOVERY
SYLVAN SH
KEEL FM
COCHRANE FM
IDEAL QUARRY MBR
35-1
Paleofavosites adaensis
u
SECTION 35 (HENRY HOUSE FALLS)
23-5
23-3
B. BEDS 23-2
23-2a
Propora thebesensis
Protaraea sp. A
Catenipora lawrencica
Aulopora sp. A
Halysites alexandricus
Paleofavosites subelongus
Propora savagei
Palaeophyllum sp
c u u c r c r c u u r
SECTION 23 (LAWRENCE QUARRY)
Paleofavosites adaensis
r
25-1
Halysites alexandricus
r
SECTION 25 (HUNTON)
24-3
LAMINATED CALCILUTITE UNIT
Halysites alexandricus
r
SECTION 24 (COAL CREEK)
21-1b
Paleofavosites subelongus
r
SECTION 21 (ROCK CROSSING)
1 m

Text-figure 2.—Locality map (A) and stratigraphic sections (to scale) in south-central Oklahoma (see Text-fig. 1A, foldout inside front cover). For legend, see Text-figure 1B. *B.* = *Brevilamnulella.* Occurrences of species in *Brevilamnulella* beds (Section-interval 23-2) and in oölite lateral to *Brevilamnulella* beds (Section-interval 23-2a) are indicated by abundance symbols on left and right sides, respectively, of range lines beside those intervals. For references and precise locations of sections, see *Appendix* (p. 104).

The Pettit Formation is a thin oölitic unit that occurs locally in northeastern Oklahoma (Amsden, 1980, pp. 23, 24). Identifiable fossils have not been recovered from this formation, and correlation with the Keel Formation is tentative. Colonial coralla were not found in our examination of a bulk rock sample from the Pettit at section Ch4 of Amsden and Rowland (1965, pp. 24, 95, 96, fig. 7, pl. B), located about 100 m north of the type section near Qualls (see Text-fig. 1A, detail map, foldout inside front cover).


B
Gilbert
33
BUFFALO R
SEARCY CO
Marshall
0 km 5
UPPER ORDOVICIAN
LOWER SILURIAN
GAMACHIAN
LLANDOVERY
CASON SH
CASON "BRASSFIELD" LST
33-1
r
1 m
Halysites alexandricus
SECTION 33 (BUFFALO RIVER)

Text-figure 3.—Locality map (B) and stratigraphic section in western north-central Arkansas (see Text-fig. 1A, foldout inside front cover). For legend, see Text-figure 1B. For references and precise location of section, see *Appendix* (p. 104).

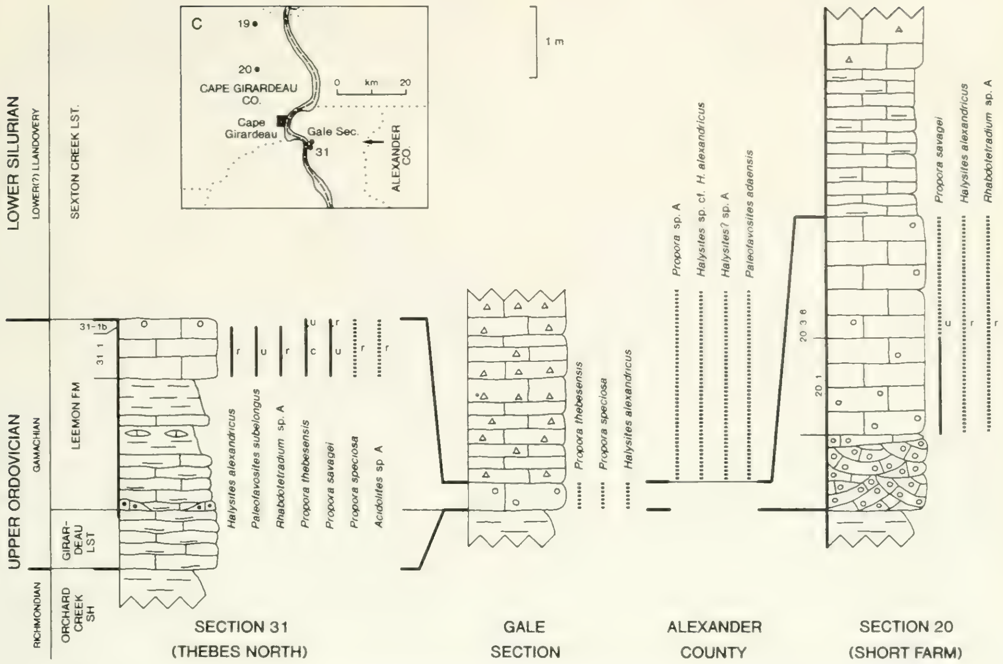
Western North-Central Arkansas

Lemastus (1979, pp. 42, 88) noted the presence of silicified corals in uppermost layers of the Cason Shale at Section 33 (Buffalo River). McAuley and Elias (1990, p. 10) reported a halysitid from those strata. The latter corallum, which we identify as *Halysites alexandricus,* occurs in chert that represents a silicified oölite (Text-fig. 3). We did not observe corals in the Cason "Brassfield" Limestone above the Cason Shale at Section 33. Maher and Lantz (1952, pp. 5, 6) reported unidentifiable solitary corals, but no colonial forms, from the "Brassfield" at a locality about 3 km to the east.

The Cason Shale at Section 33 (Buffalo River) has been correlated with the Cason Oölite at St. Clair Spring in eastern north-central Arkansas (see McAuley and Elias, 1990, pp. 9, 10, 55, fig. 3; Text-fig. 1A, detail map, foldout inside front cover). We did not find colonial coralla in the oölitic unit at that locality.

Southern Illinois and Southeastern Missouri

Uppermost Ordovician to lowermost Silurian stratigraphy in this area is shown in Text-figure 4. Corals are not known to occur in the Girardeau Limestone, and colonial forms are not known from the Orchard Creek Shale. The following colonial corals have been identified previously from the Leemon Formation at or near Section 31 (Thebes North): undetermined *Heliolites* Dana (Worthen, 1866, p. 127; unit referred to


C
19
20
CAPE GIRARDEAU CO.
Cape Girardeau
Gale Sec.
31
ALEXANDER CO.
0 km 20
1 m
LOWER SILURIAN
LOWER(?) LLANDOVERY
SEXTON CREEK LST.
UPPER ORDOVICIAN
GAMACHIAN
LEEMON FM
GIRARDEAU LST
RICHMONDIAN
ORCHARD CREEK SH
31-1b
31-1
Halysites alexandricus
Paleofavosites subelongus
Rhabdotetradium sp. A
Propora thebesensis
Propora savagei
Propora speciosa
Acidolites sp. A
Propora sp. A
Halysites sp. cf. H. alexandricus
Halysites? sp. A
Paleofavosites adaensis
20-3-8
20-1
r
u
c
SECTION 31 (THEBES NORTH)
GALE SECTION
ALEXANDER COUNTY
SECTION 20 (SHORT FARM)

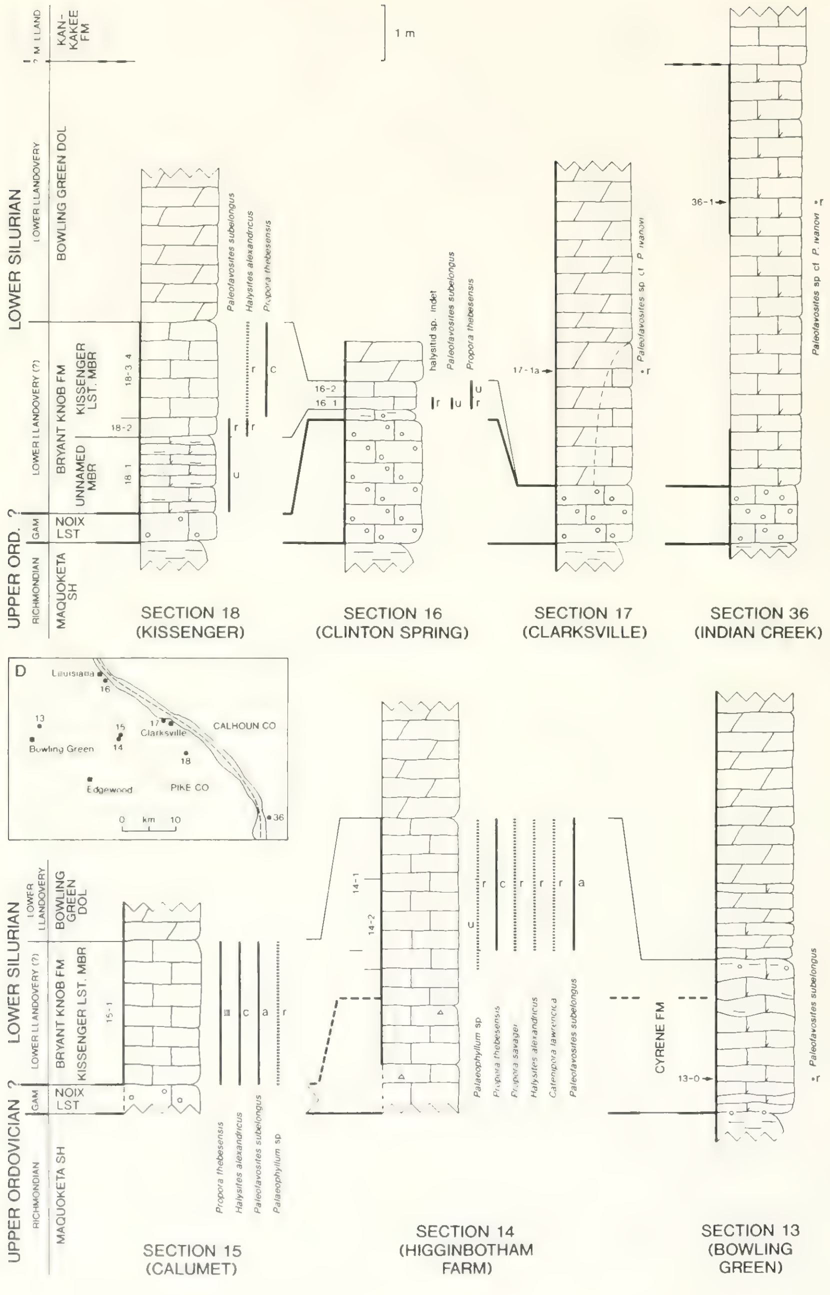
Text-figure 4.—Locality map (C) and stratigraphic sections (to scale) in southern Illinois and southeastern Missouri (see Text-fig. 1A, foldout inside front cover). For legend, see Text-figure 1B. For references and precise locations of sections, see *Appendix* (p. 104); for information on Sexton Creek corals in Alexander County, see text.

as lowermost Clear Creek Limestone therein); *Lyellia thebesensis* (Foerste, 1909, p. 95); and *L. thebesensis, Calvinia edgewoodensis* Savage, *Favosites subelongus* Savage, and *Calapoecia favositoidea* Savage (Savage, 1913, pp. 20, 24; 1917, pp. 78, 82; Edgewood Formation therein). *Lyellia thebesensis* and *C. edgewoodensis* have been reported from the Leemon at the Gale Section (Savage, 1913, p. 21; 1917, p. 79; Edgewood Formation therein). They were referred to as *Plasmopora thebesensis* (Foerste) and *Heliolites? edgewoodensis* in Savage (1910, p. 333).

Based on studies of our own collections as well as those of Foerste and of Savage, we recognize the following species in the Leemon Formation: *Propora thebesensis, Propora savagei, Propora speciosa* (Billings), *Acidolites* sp. A, *Halysites alexandricus, Paleofavosites subelongus,* and *Rhabdotetradium* sp. A. *Calvinia edgewoodensis* is a synonym of *P. speciosa* (see *Discussion,* pp. 60, 61), and *Calapoecia favositoidea* is a synonym of *P. subelongus* (see *Discussion,* p. 87). The distribution of these corals is shown in Text-figure 4. We did not find colonial coralla in the Leemon at Section 19 (New Wells).

Favosites favosus and *Halysites catenulatus* [*sic*] (Linnaeus) were identified previously from the Sexton Creek Limestone at a locality 5.8 km south of Section 31 (Thebes North) (Savage, 1913, p. 16; 1917, p. 74). We recognize the following colonial corals in Savage's collections from that unit in Alexander County, Illinois: *Propora* sp. A, *Halysites* sp. cf. *H. alexandricus, Halysites*? sp. A, and *Paleofavosites adaensis* (Text-fig. 4). Specimens were not found during our examination of the lower Sexton Creek at Section 19 (New Wells) or Section 20 (Short Farm).

Birkhead (1967, p. 28) reported *Halysites* sp., *Heliolites* sp., and *Lyellia* sp. from two localities in Cape Girardeau County, Missouri. The strata were assigned to the Sexton Creek Formation at one locality and to the Cyrene Member of the Edgewood Formation at the other. His photograph of the latter locality, showing irregular beds of chert (Birkhead, 1967, fig. 5), suggests that it is also Sexton Creek Limestone. Illustrations of


UPPER ORD.
LOWER SILURIAN
RICHMONDIAN
GAM
LOWER LLANDOVERY (?)
LOWER LLANDOVERY
? M LLAND
MAQUOKETA SH
NOIX LST
UNNAMED MBR
KISSENGER LST. MBR
BRYANT KNOB FM
BOWLING GREEN DOL
KAN-KAKEE FM
1 m
18-1
18-2
18-3 4
Paleofavosites subelongus
Halysites alexandricus
Propora thebesensis
u
r
c
16-1
16-2
halysitid sp. indet
Paleofavosites subelongus
Propora thebesensis
17-1a
Paleofavosites sp cf P. ivanovi
36-1
SECTION 18 (KISSENGER)
SECTION 16 (CLINTON SPRING)
SECTION 17 (CLARKSVILLE)
SECTION 36 (INDIAN CREEK)
D
Louisiana
16
13
15
14
17
Clarksville
CALHOUN CO
Bowling Green
18
Edgewood
PIKE CO
36
0 km 10
UPPER ORDOVICIAN
LOWER SILURIAN
LOWER LLANDOVERY
MAQUOKETA SH
NOIX LST
BRYANT KNOB FM
KISSENGER LST. MBR
BOWLING GREEN DOL
15-1
Propora thebesensis
Halysites alexandricus
Paleofavosites subelongus
Palaeophyllum sp
a
14-1
14-2
Palaeophyllum sp
Propora thebesensis
Propora savagei
Halysites alexandricus
Catenipora lawrencica
Paleofavosites subelongus
CYRENE FM
13-0
SECTION 15 (CALUMET)
SECTION 14 (HIGGINBOTHAM FARM)
SECTION 13 (BOWLING GREEN)

coralla from that locality, identified by Birkhead as *Lyellia* sp. (Birkhead, 1967, pl. 4, figs. 4a, 4b) and *Heliolites* sp. (Birkhead, 1967, pl. 4, figs. 5a, 5b), show a probable *Propora* Milne-Edwards and Haime and a questionable representative of the family Coccoserididae Kiaer, respectively. The specimens have not been located (Carter, oral commun., 1992).

WEST-CENTRAL ILLINOIS AND NORTHEASTERN MISSOURI

Uppermost Ordovician to lowermost Silurian stratigraphy in this area is shown in Text-figure 5. Corals are not known from the Maquoketa Shale in west-central Illinois and northeastern Missouri. The following colonial (or possibly colonial) corals have been identified previously from strata that represent the combined Noix Limestone and Bryant Knob Formation in northeastern Missouri: *Acervularia Davidsoni?* [*sic*] Milne-Edwards and Haime (Swallow, 1855, p. 107; unit referred to as Oölitic Limestone therein); *Halysites catenulata* [*sic*] (Linnaeus), *Favosites* sp? [*sic*], and *Cyathophyllum* sp? [*sic*] (Rowley, 1908, p. 23; oölitic limestone therein); and *Lyellia thebesensis, Halysites catenulatus* [*sic*], *Favosites subelongus,* and *Calapoecia favositoidea* (Savage, 1913, p. 24; 1917, p. 82; Noix Oölite therein). *Halysites* Fischer von Waldheim has been noted in blocks considered to be from the Noix Limestone (Amsden, 1974, fig. 9). The following have been identified from strata that represent the combined Cyrene Formation and Bowling Green Dolomite in northeastern Missouri: *Lyellia?* sp? [*sic*], *H. catenulata, Favosites* sp? [*sic*], *Columnaria* sp? [*sic*], and *Cyathophyllum* sp? [*sic*] (Rowley, 1908, p. 23; brown, earthy limestone therein); and *L. thebesensis, F. subelongus,* and *C. favositoidea* (Savage, 1913, p. 24; 1917, p. 82; Edgewood Formation therein). *Lyellia thebensis* [*sic*] (Foerste) was listed from the Bowling Green in west-central Illinois by Rubey (1952, p. 170).

Our understanding of colonial corals and their distribution in this area is based on collections made during the present study (Text-fig. 5), and on our examination of material collected by T. E. Savage (University of Illinois at Urbana–Champaign collection). We have not found colonial coralla in the Noix Limestone. *Paleofavosites subelongus* is the only species known from the unnamed member of the Bryant Knob Formation. The following are present in the Kissenger Limestone Member of the Bryant Knob: *Propora thebesensis, Propora savagei, Halysites alexandricus, Catenipora lawrencica, P. subelongus,* and *Palaeophyllum* sp. *Calapoecia favositoidea* is a synonym of *P. subelongus* (see *Discussion,* p. 87). We obtained *P. subelongus* from the Cyrene Formation at Section 13 (Bowling Green). The only colonial coral known from the Bowling Green Dolomite is *Paleofavosites* sp. cf. *P. ivanovi* Sokolov.

In Savage's collections made near Edgewood, Missouri (see Text-fig. 5, locality map), we identify the colonial corals *Propora thebesensis, Propora savagei, Plasmopora* sp. cf. *P. logani* Young and Noble, and *Paleofavosites subelongus.* All are considered to be from the Cyrene Formation, and not from the Bowling Green Dolomite. This is based on statements by Savage (1913, pp. 22, 64, 65; 1917, pp. 80, 114, 115), on the lithology of matrix adhering to one specimen, on the absence of these species in known Bowling Green beds, on the presence of *P. subelongus* in known Cyrene strata, and on the occurrence of *P. thebesensis, P. savagei,* and *P. subelongus* in the Bryant Knob Formation, which together with the Noix Limestone is a lateral equivalent of the Cyrene (see McAuley and Elias, 1990, p. 15).

NORTHEASTERN ILLINOIS

Uppermost Ordovician to lowermost Silurian stratigraphy in this area is shown in Text-figure 6. Corals are not known from the Maquoketa Group in northeastern Illinois. The following colonial corals have been identified previously from the Wilhelmi Formation at Section 37 (Essex): *Halysites catenulatus* [*sic*] and *Favosites* cf. *niagarensis* (Savage, 1912, p. 100; 1913, p. 29; 1917, p. 87; unit referred to as Essex Limestone therein); and *Lyellia* cf. *thebesensis* and *F. niagarensis* (Athy, 1928, p. 40; Essex Limestone therein). From loose blocks of the Wilhelmi at that section, we recovered *Halysites alexandricus, Paleofavosites subelongus,* and *Aulopora* sp. A. One poorly preserved favositid corallum, referred to as *Paleofavosites* sp. indet., was found in the upper portion of the Schweizer Member of the Wilhelmi Formation at Section 4 (Schweizer West).

Savage (1914, p. 31) identified *Lyellia thebesensis* from 3.2 km and 5.6 km south of Channahon, Illinois (see Text-fig. 6, locality map). We have studied his collections from the former locality, and recognize *Pro-*

←

Text-figure 5.—Locality map (D) and stratigraphic sections (to scale) in west-central Illinois and northeastern Missouri (see Text-fig. 1A, foldout inside front cover). For legend, see Text-figure 1B. Gam. = Gamachian. Abundance symbols on left and right sides of range line for *Palaeophyllum* sp. at Section 14 (Higginbotham Farm) refer to Section-intervals 14-2 and 14-1, respectively. For references and precise locations of sections, see *Appendix* (pp. 104, 105).

pora thebesensis, Halysites alexandricus, and *Paleofavosites subelongus.* They are considered to be from the Wilhelmi Formation. The matrix of one specimen contains a corallum of the solitary rugosan *Streptelasma subregulare* (Savage), which is restricted to the Wilhelmi in this area (see McAuley and Elias, 1990, p. 20, fig. 7).

From the Elwood Formation, we recovered *Propora* sp. aff. *P. affinis* (Billings) and *Paleofavosites* sp. A. The distribution of colonial corals found in the Wilhelmi and Elwood formations during the present study is shown in Text-figure 6. We did not observe colonial coralla in the Wilhelmi at Section 3 (Garden Prairie), or in the Wilhelmi and lower Elwood at Section 34 (Belvidere South).

NORTHWESTERN ILLINOIS AND EASTERN IOWA

Uppermost Ordovician to lowermost Silurian stratigraphy in this area is shown in Text-figure 7. Colonial corals are not known from the Brainard Shale in northwestern Illinois and eastern Iowa. In the Mosalem Formation at Section 32 (Thomson East), *Pycnostylus*? sp. was previously identified from the fill of small, local channels (McAuley and Elias, 1990, p. 22, fig. 9; Section-interval 32-1b). We document it as *Pycnostylus* sp. A. The presence of tabulate corals in a bed on the old quarry floor was reported by McAuley and Elias (1990, p. 22; Section-interval 32-1z). We obtained *Propora thebesensis, Halysites alexandricus,* and *Paleofavosites subelongus* from that coral-rich bedding surface, which appears to be at about the same stratigraphic position as the top of the channels. *Propora thebesensis, Propora speciosa,* and *Paleofavosites* sp. cf. *P. subelongus* were found in the upper Mosalem, above the filled channels (Section-interval 32-1c). At Section 10 (Lost Mound), *Paleofavosites adaensis* occurs near the top of the Mosalem. The distribution of these corals is shown in Text-figure 7.

We found poorly preserved specimens, identified as favositid sp. indet., 3.3 m below the top of the Mosalem Formation at both Section 8 (King) and Section 30 (Thomson Northeast). Colonial coralla were not observed in the Mosalem at Section 9 (Winston), Section 11 (Schapville), Section 12 (Stockton), or Section 26 (Bellevue).

COLONIAL CORAL ASSEMBLAGES

The stratigraphic and geographic distribution of colonial corals in uppermost Ordovician to lowermost Silurian sequences within the east-central United States is summarized in Text-figure 8 (foldout inside back cover). We recognize two assemblages. The Edgewood Assemblage (Table 1) includes colonial corals representing 13 species and 11 genera. Tabulates of five orders account for over 95% of specimens; the remainder are colonial rugosans of a single order. A total of 84% of specimens belong to the following three species: *Paleofavosites subelongus, Propora thebesensis,* and *Halysites alexandricus.* In addition to being numerically dominant, these species are also the most widely distributed; *H. alexandricus* occurs in all six outcrop areas. Stratigraphically, the Edgewood Assemblage is situated above Upper Ordovician Richmondian beds that are not known to contain colonial corals in the study region.

The Edgewood Assemblage is succeeded by a Silurian assemblage that includes tabulates belonging to *Propora, Halysites,* and *Paleofavosites* Twenhofel (Table 2). Although these genera are represented in both the Silurian and Edgewood assemblages, the characteristic species are different. *Paleofavosites adaensis* is the most widely distributed Silurian form, occurring in south-central Oklahoma as well as southern and northwestern Illinois. *Halysites* sp. cf. *H. alexandricus* and *Paleofavosites* sp. cf. *P. subelongus* of the Silurian assemblage are comparable to Edgewood taxa. Colonial corals of the Edgewood and Silurian assemblages are known to co-occur at only one locality, Section 32 (Thomson East) (see Text-fig. 7). There, *Propora thebesensis* and *Propora speciosa* are found with *Paleofavosites* sp. cf. *P. subelongus* in the upper Mosalem Formation. *Paleofavosites adaensis,* which is characteristic of the Silurian assemblage, is present in the upper Mosalem at Section 10 (Lost Mound).

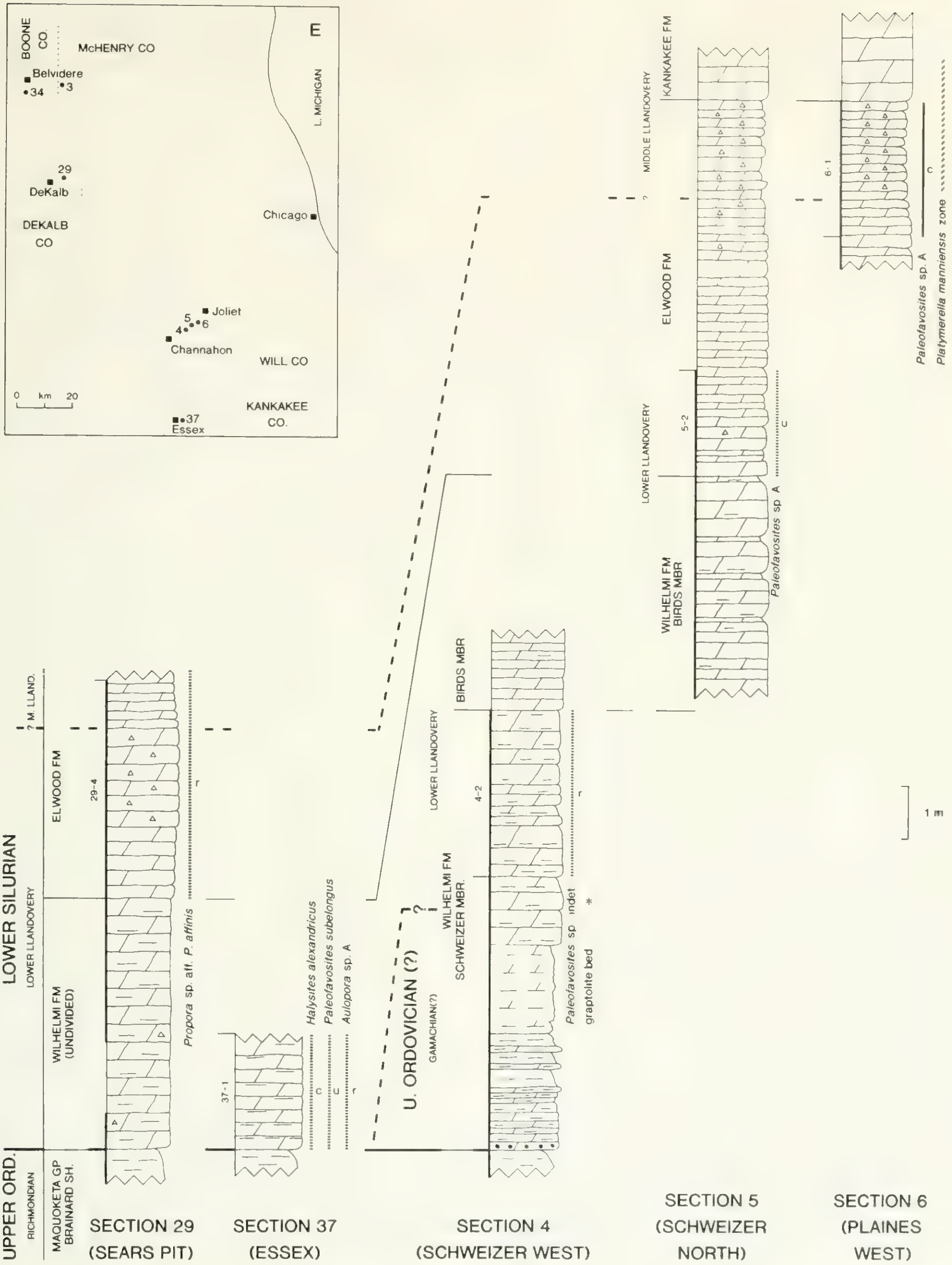
It is noteworthy that solitary rugose corals of the Silurian assemblage represent different genera from those in the Edgewood Assemblage (McAuley and Elias, 1990, table 1). Rugosan species of the two assemblages are not known to co-occur (Elias, 1992, p. 120).

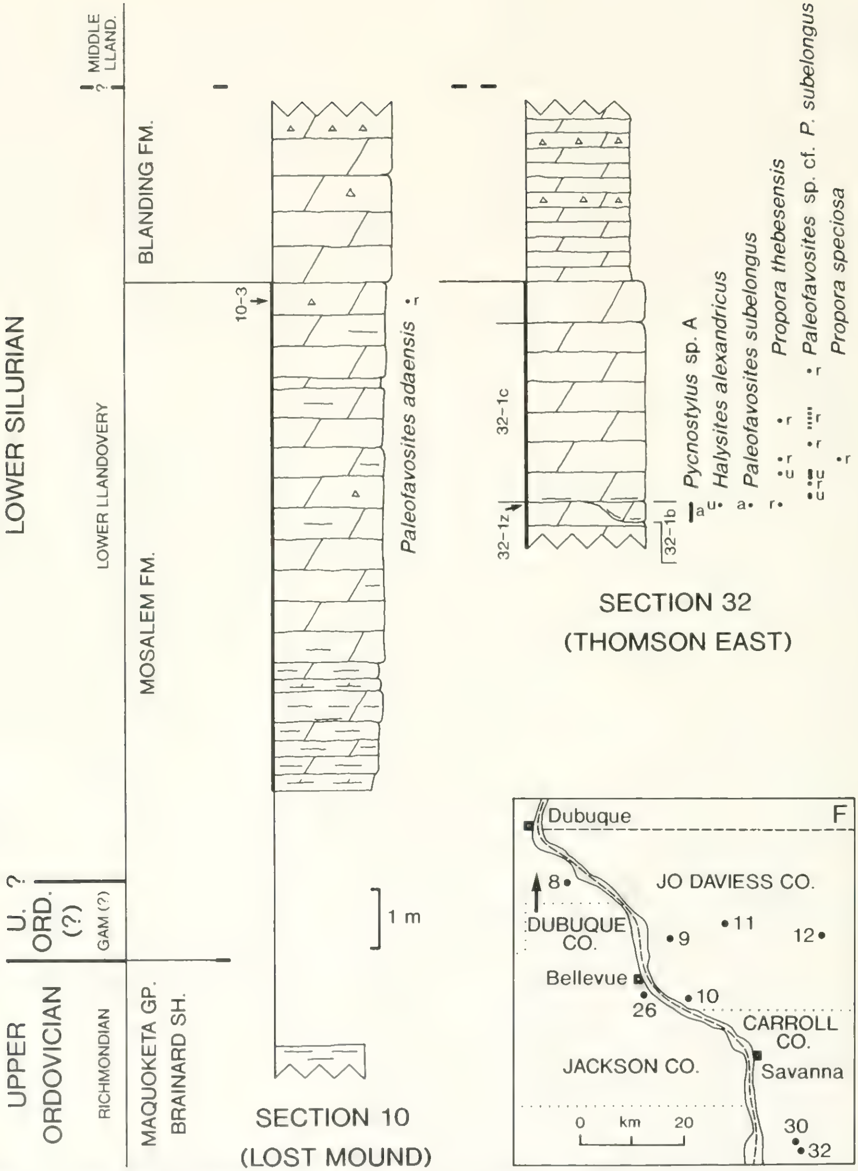
AGE OF UNITS AND REGIONAL CORRELATION

The age and correlation of uppermost Ordovician to lowermost Silurian strata in the east-central United States are summarized in Text-figure 8 (foldout inside back cover). The evidence, based on brachiopods, conodonts, corals, graptolites, lithology, stratigraphic position, and sea-level curves, has been discussed in detail by McAuley and Elias (1990), Elias and Young

→

Text-figure 6.—Locality map (E) and stratigraphic sections (to scale) in northeastern Illinois (see Text-fig. 1A, foldout inside front cover). For legend, see Text-figure 1B. For references and precise locations of sections, see *Appendix* (p. 105).


E
BOONE CO.
McHENRY CO
Belvidere
34
3
L. MICHIGAN
29
DeKalb
DEKALB CO
Chicago
Joliet
5
6
4
Channahon
WILL CO
0 km 20
37
Essex
KANKAKEE CO.
UPPER ORD.
RICHMONDIAN
MAQUOKETA GP BRAINARD SH.
LOWER SILURIAN
LOWER LLANDOVERY
? M. LLAND.
WILHELMI FM (UNDIVIDED)
ELWOOD FM
29-4
Propora sp. aff. P. affinis
r
SECTION 29 (SEARS PIT)
37-1
Halysites alexandricus
Paleofavosites subelongus
Aulopora sp. A
c
u
r
SECTION 37 (ESSEX)
U. ORDOVICIAN (?)
GAMACHIAN(?)
?
WILHELMI FM SCHWEIZER MBR.
LOWER LLANDOVERY
BIRDS MBR
4-2
Paleofavosites sp. indet
graptolite bed
*
r
SECTION 4 (SCHWEIZER WEST)
MIDDLE LLANDOVERY
?
KANKAKEE FM
ELWOOD FM
LOWER LLANDOVERY
5-2
WILHELMI FM BIRDS MBR
Paleofavosites sp. A
u
SECTION 5 (SCHWEIZER NORTH)
6-1
c
Paleofavosites sp. A
Platymerella manniensis zone
SECTION 6 (PLAINES WEST)
1 m


LOWER SILURIAN
UPPER ORDOVICIAN
U. ? ORD. (?)
MIDDLE LLAND.
LOWER LLANDOVERY
RICHMONDIAN
GAM (?)
BLANDING FM.
MOSALEM FM.
MAQUOKETA GP.
BRAINARD SH.
10-3
Paleofavosites adaensis
r
1 m
SECTION 10
(LOST MOUND)
32-1c
32-1z
32-1b
Pycnostylus sp. A
Halysites alexandricus
Paleofavosites subelongus
Propora thebesensis
Paleofavosites sp. cf. P. subelongus
Propora speciosa
a u a r r u c r r r r
SECTION 32
(THOMSON EAST)
Dubuque
F
8
JO DAVIESS CO.
DUBUQUE CO.
9
11
12
Bellevue
26
10
CARROLL CO.
JACKSON CO.
Savanna
0 km 20
30
32

Text-figure 7.—Locality map (F) and stratigraphic sections (to scale) in northwestern Illinois and eastern Iowa (see Text-fig. 1A, foldout inside front cover). For legend, see Text-figure 1B. Gam. = Gamachian. Occurrences of species in Section-interval 32-1z are indicated by abundance symbols on left sides of range lines beside that interval. For references and precise locations of sections, see *Appendix* (pp. 105, 106).

Table 1.—Colonial corals of the Edgewood Assemblage, relative abundance based on all identified specimens (n = 324), and distribution in outcrop areas within the east-central United States. Specimens are individual coralla except for two of the three specimens of *Aulopora* sp. A, which appear to include several coralla, and the eight specimens of *Pycnostylus* sp. A, each of which includes several dissociated corallites. *A* = south-central Oklahoma, *B* = western north-central Arkansas, *C* = southern Illinois and southeastern Missouri, *D* = west-central Illinois and northeastern Missouri, *E* = northeastern Illinois, *F* = northwestern Illinois and eastern Iowa (see Text-fig. 1A, foldout inside front cover); × indicates an occurrence.

		distribution					
taxa	*relative abundance*	*A*	*B*	*C*	*D*	*E*	*F*
Subclass Tabulata	95.6%						
Order Heliolitida	33.5%						
Family Proporidae							
Propora thebesensis	25.9%	×	—	×	×	×	×
Propora savagei	4.9%	×	—	×	×	—	—
Propora speciosa	1.2%	—	—	×	—	—	—
Family Plasmoporidae							
Plasmopora sp. cf. *P. logani*	0.3%	—	—	—	×	—	—
Family Coccoserididae							
Acidolites sp. A	0.3%	—	—	×	—	—	—
Protaraea sp. A	0.9%	×	—	—	—	—	—
Order Halysitida	15.5%						
Family Halysitidae							
Halysites alexandricus	13.3%	×	×	×	×	×	×
Catenipora lawrencica	2.2%	×	—	—	×	—	—
Order Favositida	44.8%						
Suborder Favositina							
Superfamily Favositicae							
Family Favositidae							
Subfamily Favositinae							
Paleofavosites subelongus	44.8%	×	—	×	×	×	×
Order Auloporida	0.9%						
Superfamily Auloporicae							
Family Auloporidae							
Aulopora sp. A	0.9%	×	—	—	—	×	—
Order Tetradiida	0.9%						
Family Tetradiidae							
Rhabdotetradium sp. A	0.9%	—	—	×	—	—	—
Subclass Rugosa	4.4%						
Order Stauriida	4.4%						
Suborder Stauriina							
Family Stauriidae							
Palaeophyllum sp.	1.9%	×	—	—	×	—	—
Family Pycnostylidae							
Pycnostylus sp. A	2.5%	—	—	—	—	—	×

(1992), and Elias (1992). Here, we consider the biostratigraphic significance of colonial corals in the Edgewood and Silurian assemblages.

Two of the Edgewood proporids are known to occur outside the east-central United States. *Propora thebesensis* is present in the Ellis Bay Formation (uppermost Ordovician, Gamachian, to possibly lowermost Silurian, Lower Llandovery, lowermost Rhuddanian) and in the overlying Becscie Formation (Rhuddanian) on Anticosti Island, Québec (see *Discussion,* p. 53). It may also occur in the Grande Coupe beds (Upper Ordovician, Ashgill, pre-Hirnantian) of the Matapédia Group on the Gaspé Peninsula, Québec, and in the Manitoulin Formation (Rhuddanian) of southern Ontario. *Propora speciosa* is found in the Ellis Bay Formation and possibly in the Grande Coupe beds (see *Discussion,* pp. 60, 61). It may also be present in the Tsagan-Del beds (Ashgill) of Mongolia, and in the Porkuni Stage (Hirnantian; *i.e.,* upper Gamachian) of Estonia. The Edgewood favositid *Paleofavosites subelongus* possibly occurs in basal strata of the Becscie Formation (see *Discussion,* p. 87). Thus, tabulate corals are consistent with the interpretation that strata containing the Edgewood Assemblage in the east-central United States are Gamachian to early Rhuddanian in age.

In northeastern Illinois, colonial corals of the Silurian assemblage appear in the lower Elwood Formation (see Text-fig. 6). This is above a bed in the underlying Wilhelmi Formation that contains Early Llandovery

Table 2.—Colonial corals of the Silurian assemblage in the study region, east-central United States.

- Subclass Tabulata
  - Order Heliolitida
    - Family Proporidae
      - *Propora thebesensis*
      - *Propora speciosa*
      - *Propora* sp. aff. *P. affinis*
      - *Propora* sp. A
  - Order Halysitida
    - Family Halysitidae
      - *Halysites* sp. cf. *H. alexandricus*
      - *Halysites*? sp. A
  - Order Favositida
    - Suborder Favositina
      - Superfamily Favositicae
        - Family Favositidae
          - Subfamily Favositinae
            - *Paleofavosites adaensis*
            - *Paleofavosites* sp. cf. *P. subelongus*
            - *Paleofavosites* sp. cf. *P. ivanovi*
            - *Paleofavosites* sp. A

graptolites possibly representing the earliest Rhuddanian *Parakidograptus acuminatus* Zone (Ross, 1962; Berry and Boucot, 1970, p. 145). The *Platymerella manniensis* brachiopod zone, which is considered to mark the Middle Llandovery (Berry and Boucot, 1970, pl. 2), begins in the upper Elwood (Willman, 1973, p. 14). In eastern Iowa, Early Llandovery graptolites in a bed near the base of the Mosalem Formation apparently represent the same zone as those in the Wilhelmi (Ross, 1964). The Mosalem as well as overlying strata have been placed in the Rhuddanian on the basis of correlations involving sea-level curves (Johnson *et al.*, 1985, fig. 5). Colonial corals characteristic of the Silurian assemblage appear in the upper Mosalem of northwestern Illinois, which has been correlated with the lower Elwood on the basis of solitary corals and stratigraphic position (McAuley and Elias, 1990, p. 26). We conclude that colonial corals of the Silurian assemblage appeared in the east-central United States during late Rhuddanian time, and underlying Silurian strata containing corals representing only the Edgewood Assemblage are early Rhuddanian in age.

A total of 11 of the 13 colonial coral species in the Edgewood Assemblage are known from Gamachian strata of the Leemon Formation in southern Illinois and southeastern Missouri, the Cason Shale in western north-central Arkansas, and the lower Keel Formation in south-central Oklahoma (*i.e.*, excluding Section-interval 24-3; see Text-fig. 2): *Propora thebesensis*, *Propora savagei*, *Propora speciosa*, *Acidolites* sp. A, *Protaraea* sp. A, *Halysites alexandricus*, *Catenipora lawrencica*, *Paleofavosites subelongus*, *Aulopora* sp. A, *Rhabdotetradium* sp. A, and *Palaeophyllum* sp. We consider them to have appeared in the east-central United States during latest Ordovician time. Three of the species, *P. thebesensis*, *H. alexandricus*, and *P. subelongus*, are known to range into the early Rhuddanian, when *Pycnostylus* sp. A appeared. These colonial corals occur in Section-intervals 32-1z and 32-1b of the Mosalem Formation (see Text-fig. 7), in association with the characteristic Edgewood solitary rugosan *Streptelasma subregulare* (see McAuley and Elias, 1990, p. 22; Elias, 1992, p. 120). Their stratigraphic position projects above a bed containing Early Llandovery graptolites near the base of the Mosalem at Section 26 (Bellevue) (see Elias, 1992, fig. 6).

In northeastern Missouri, the Edgewood species *Propora thebesensis*, *Propora savagei*, *Plasmopora* sp. cf. *P. logani*, and *Paleofavosites subelongus* occur in the Cyrene Formation near Edgewood, but their stratigraphic positions within the unit are unknown. The lower to middle portion of this formation is Gamachian, but the upper part may be Early Llandovery (see McAuley and Elias, 1990, pp. 17, 25, 26). Therefore, it is uncertain whether *Plasmopora* sp. cf. *P. logani* appeared during the latest Ordovician or the earliest Silurian. We consider specimens of *P. subelongus* from Section-interval 13-0 near the base of the Cyrene to be Gamachian (see Text-fig. 5). They occur below an interval containing the conodont *Noixodontus girardeauensis* (Satterfield) (see Thompson and Satterfield, 1975, fig. 11), which indicates a latest Ordovician age (see Barrick, 1986, pp. 64, 66). Strata of the Bryant Knob Formation that contain corals of the Edgewood Assemblage are tentatively considered to be Early Llandovery, although a Gamachian age cannot be ruled out (see McAuley and Elias, 1990, pp. 17, 26). Therefore, coralla of *P. subelongus* in the unnamed member and *P. thebesensis*, *P. savagei*, *Halysites alexandricus*, *Catenipora lawrencica*, *P. subelongus*, and *Palaeophyllum* sp. in the Kissenger Limestone Member are questionably early Rhuddanian.

In northeastern Illinois, we recovered a single colonial corallum from the sequence through the Wilhelmi Formation at Section 4 (Schweizer West) and Section 5 (Schweizer North). It was found in Section-interval 4-2, a small distance above a bed that contains Early Llandovery graptolites possibly representing the earliest Rhuddanian *Parakidograptus acuminatus* Zone (see Text-fig. 6). The coral is therefore assigned a Silurian age, but unfortunately can only be identified as *Paleofavosites* sp. indet. The characteristic Edgewood solitary rugosan *Streptelasma subregulare* is known to occur below the graptolite bed, and it is possible that those strata are Gamachian (see Elias, 1992, p. 118, fig. 4). The Edgewood colonial species *Propora the-*

besensis, Halysites alexandricus, Paleofavosites subelongus, and *Aulopora* sp. A are known from the Wilhelmi at other localities, but their stratigraphic positions with respect to the graptolite bed at Section 4 are unknown. These coralla are early Rhuddanian or questionably Gamachian in age.

The Bowling Green Dolomite of west-central Illinois and northeastern Missouri has been correlated with the lower Elwood Formation of northeastern Illinois, which is considered to be late Rhuddanian in age. Correlation of these strata is based on their position between units containing Edgewood Assemblage corals (below) and the *Platymerella manniensis* Zone (above), and on the occurrence in these strata of corals representing the Silurian assemblage (see McAuley and Elias, 1990, p. 26). *Paleofavosites* sp. cf. *P. ivanovi,* the only colonial coral known from the Bowling Green, is therefore considered to be late Rhuddanian. As is the case for corals, there appears to be a significant difference in brachiopod assemblages between the Bowling Green Dolomite and the underlying Bryant Knob Formation (see Stanton *et al.,* 1990).

The lower part of the Sexton Creek Limestone in southern Illinois and southeastern Missouri could be the same age as the Bowling Green Dolomite in west-central Illinois and northeastern Missouri (*i.e.,* Early Llandovery, late Rhuddanian). Both contain conodonts representing the *Paltodus dyscritus* fauna (Thompson and Satterfield, 1975, figs. 6, 7, 9, 11–15) and solitary rugose corals of the Silurian assemblage (McAuley and Elias, 1990, p. 26). *Stricklandia protriplesiana* (Amsden) has been identified from the Sexton Creek by Amsden (1974, p. 24; 1986, p. 26; 1988, p. 26). The presence of this brachiopod suggests a younger age (Late Llandovery, C_{1-2}), but its stratigraphic position within the formation is not known. The colonial corals *Propora* sp. A, *Halysites* sp. cf. *H. alexandricus, Halysites*? sp. A, and *Paleofavosites adaensis* occur in the Sexton Creek. They represent the Silurian assemblage, but their stratigraphic positions are unknown. *Paleofavosites adaensis* is also present in the upper Mosalem Formation of northwestern Illinois, suggesting correlation with those strata, which are considered to be late Rhuddanian. An upper limit on the range of *P. adaensis,* however, has not been established. The lower Sexton Creek is questionably assigned a late Rhuddanian age.

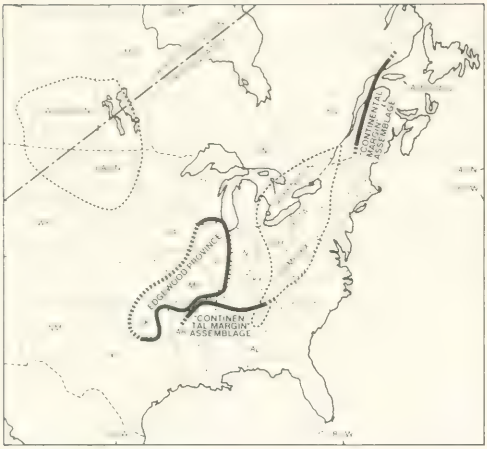
In the upper Keel Formation of south-central Oklahoma (Section-interval 24-3; see Text-fig. 2), the Edgewood colonial coral *Halysites alexandricus* occurs with the solitary rugosan *Streptelasma subregulare* (see Elias, 1992, p. 114, fig. 2). A conodont fauna of general Silurian aspect that appears in the same bed was considered to be Llandovery by Barrick (1986, p. 67), although a latest Ordovician age cannot be ruled out (see Bergström and Boucot, 1988, pp. 278, 279; McAuley and Elias, 1990, pp. 8, 9). Therefore, we consider the corallum of *H. alexandricus* from that interval to be of questionable early Rhuddanian age. In the east-central United States, the change in conodont faunas from those of Ordovician to those of Silurian aspect occurred during the range of the Edgewood coral assemblage, prior to the appearance of corals representing the Silurian assemblage.

Basal strata of the Cochrane Formation in south-central Oklahoma are evidently diachronous. Conodonts at the base of the formation, including those at Section 21 (Rock Crossing) and Section 23 (Lawrence Quarry), were considered to be Llandovery (position uncertain) by Barrick (1986, pp. 57, 64, 67). At Section 21, the characteristic Edgewood solitary rugosan *Streptelasma subregulare* occurs in the basal Cochrane (Elias, 1992, p. 114, fig. 2); unfortunately, we did not find colonial corals in the lower Cochrane at that locality. Assuming those strata are Llandovery (and not Gamachian), an early Rhuddanian age is indicated. *Paleofavosites adaensis,* the only colonial coral known from the lower Cochrane, represents the Silurian assemblage. It occurs at Section 23 and Section 35 (Henry House Falls), where solitary rugose corals in the basal Cochrane also represent the Silurian assemblage (see McAuley and Elias, 1990, p. 26, fig. 2; Elias, 1992, pp. 114, 115, fig. 2). The presence of *P. adaensis* suggests correlation with the upper Mosalem Formation of northwestern Illinois and the Sexton Creek Limestone of southern Illinois, and an age of late Rhuddanian (or possibly younger).

BIOGEOGRAPHY AND EVENTS

EDGEWOOD PROVINCE

The Edgewood Assemblage of colonial corals is strikingly different from typical Late Ordovician Richmondian assemblages in the North American cratonic interior, such as those known from the Richmondian Stage in Kentucky–Indiana–Ohio, the Cutter Dolomite in southern New Mexico–westernmost Texas, the Stony Mountain Formation in southern Manitoba, and the Churchill River Group in northeastern Manitoba (see Elias and Young, 1992, table 2; Text-fig. 9). Tabulates of the order Sarcinulida Sokolov (primarily *Calapoecia* Billings) and massive rugosans of the family Stauriidae Milne-Edwards and Haime (*Cyathophylloides* Dybowski and *Favistina* Flower) are widespread in the Richmondian but absent from the Edgewood Assemblage. *Propora* and *Halysites* are characteristic of the Edgewood Assemblage, but absent from the Richmondian assemblages. The Edgewood colonial rugo-



Text-figure 9.—Biogeographic and paleogeographic features in eastern and central North America. Latest Ordovician to earliest Silurian Edgewood Province and occurrences of Late Ordovician "continental margin" coral assemblages are shown; heavy solid and dashed lines represent established and uncertain boundaries, respectively. Late Ordovician Queenston Delta Complex and Williston Basin are outlined. Latest Ordovician paleoequator is based on Scotese and McKerrow (1990, fig. 9); present latitudes and longitudes are shown at margin. Abbreviations of states (United States): *AL* = Alabama, *AR* = Arkansas, *IA* = Iowa, *IL* = Illinois, *IN* = Indiana, *KY* = Kentucky, *MO* = Missouri, *NM* = New Mexico, *OH* = Ohio, *OK* = Oklahoma, *TX* = Texas, *WY* = Wyoming. Abbreviations of provinces (Canada): *MB* = Manitoba, *ON* = Ontario, *PQ* = Québec (Anticosti Island is identified).

sans, *Palaeophyllum* Billings and *Pycnostylus* Whiteaves, are fasciculate.

We relate the disappearance of Richmondian-type colonial corals from the cratonic interior of eastern North America to habitat loss. This resulted from westward progradation of the Queenston Delta Complex (Text-fig. 9) and from regression of the epeiric sea during a major glacio-eustatic drop in the late Richmondian. Extinctions among other groups in this region have also been linked to these events: brachiopods (Sheehan, 1973), solitary corals (Elias, 1982, pp. 48, 51; 1989; McAuley and Elias, 1990, p. 27), bryozoans (Anstey, 1986), and crinoids (Eckert, 1988). Erosional relief on the Richmondian surface of the Maquoketa Group is more than 30 m in northeastern Illinois (Willman, 1973, p. 12; Mikulic *et al.*, 1985, p. 9) and exceeds 40 m in eastern Iowa (Brown and Whitlow, 1960, p. 23; Whitlow and Brown, 1963, p. 11; see also Witzke and Kolata, 1988, pp. 61, 64, figs. 4, 5). The channels or depressions were subsequently infilled with latest Ordovician (?; Gamachian?) to earliest Silurian (Early Llandovery, Rhuddanian) deposits of the Wilhelmi and Mosalem formations. This suggests a period of emergence, at least within the northern portion of the study region in the east-central United States.

The Edgewood colonial corals *Propora savagei, Halysites alexandricus,* and *Catenipora lawrencica* are endemic, as are all solitary rugosans of the Edgewood Assemblage. The area of the east-central United States that was occupied by the Edgewood Assemblage has been named the Edgewood Province (Elias, 1982, pp. 47, 51, 52, fig. 24; McAuley and Elias, 1990, pp. 27, 28, fig. 11; Text-fig. 9). Corals were likely introduced to this biogeographic province from the continental margin, or were derived from forms previously restricted to the continental margin. *Propora,* which is present in the Richmondian Vauréal Formation on Anticosti Island, Québec (Bolton, 1981a, p. 107), appeared earlier along the continental margin than in the east-central United States. *Propora thebesensis* and *Propora speciosa* occur on Anticosti Island and in the Edgewood Province, indicating connection between the continental margin and cratonic interior. The endemic Edgewood species *Propora savagei* may have arisen from *P. thebesensis* by speciation within this province. *Halysites alexandricus* represents a genus that was introduced from elsewhere, as *Halysites* is known from earlier deposits only in Australasia (see *Discussion,* p. 70).

The Edgewood Assemblage includes the youngest North American representative of the order Tetradiida Okulitch (*Rhabdotetradium* sp. A), which is present in the latest Ordovician (Gamachian) Leemon Formation. This is among the youngest occurrences worldwide of this important Ordovician order. The Edgewood Assemblage also includes a number of first occurrences of typical Silurian taxa. The earliest North American member of the genus *Halysites* (*H. alexandricus*) appears in Gamachian strata within the Edgewood Province. The oldest definite representative of the family Plasmoporidae Sardeson (*Plasmopora* sp. cf. *P. logani*) is from Gamachian or questionably early Rhuddanian strata of the Cyrene Formation. The earliest known occurrence of the family Pycnostylidae Stumm (*Pycnostylus* sp. A) is from an early Rhuddanian bed within the Mosalem Formation.

Gamachian strata in the southern to central portion of the Edgewood Province were likely deposited during minor transgressions into the cratonic interior from the south, as sea level fluctuated during a regressive phase corresponding to the latest Ordovician glacial maximum (see Elias, 1982, pp. 51, 52; McAuley and Elias, 1990, p. 27). Immigration of colonial corals was probably related to shifts of suitable habitat areas during a time of depressed temperatures, as suggested previously for the solitary rugosans (Elias, 1989, p. 325). Corals that were introduced to the cratonic interior may have favored cooler water than did those in the Richmondian epeiric seas. Conditions were apparently within the warm, tropical to subtropical range, however, as indicated by widespread oölites and algal limestones, and the development of small biohermal mounds composed of bryozoans, brachiopods, and solitary rugose corals in the Leemon Formation at Section 19 (New Wells) in southeastern Missouri (Amsden, 1974, pp. 21, 22, fig. 17; 1986, pp. 33, 45, 54; Elias, 1989, p. 320). In the northern part of the Edgewood Province, sediment infilling channels or depressions cut into the Maquoketa Group probably accumulated during the major transgression associated with deglaciation, in latest Gamachian to Early Llandovery time (see Johnson *et al.,* 1985, fig. 5, eastern Iowa). Dispersion of Edgewood corals was evidently related to expansion of suitable habitat areas during the early phase of this event (Elias, 1989, pp. 320, 325).

The striking difference we have documented between the Edgewood Assemblage and typical Richmondian colonial coral assemblages in the North American cratonic interior probably reflects, at least in part, a hiatus between Richmondian and Gamachian deposition in the east-central United States. The most fossiliferous and complete Richmondian through Lower Llandovery sequence is in a continental margin setting on Anticosti Island, Québec (see Barnes, 1988). There, Elias and Young (1992, table 2) tabulated occurrences of corals in the Vauréal Formation (Richmondian), Ellis Bay Formation (Gamachian to possibly lowermost Rhuddanian), and lower portion of member 1 of the Becscie Formation (lower Rhuddanian). Some of the Richmondian species survived into the Gamachian. These include the massive stauriid *Cyathophylloides lyterion* Bolton and the sarcinulid *Calapoecia anticostiensis* Billings, which range from the Vauréal into the Ellis Bay and lowermost Becscie, respectively.

The Stonewall Formation overlies the Richmondian Stony Mountain Formation in southern Manitoba, within the Williston Basin area of the cratonic interior (Text-fig. 9). The Stonewall coral assemblage is a mixture of Richmondian types and newly introduced forms (see Elias, 1989, p. 322, fig. 3; Elias and Young, 1992, table 2). Sarcinulids (including *Calapoecia*) occur with one of the earliest North American representatives of the family Tryplasmatidae Etheridge (*Tryplasma* Lonsdale). Within the Williston Basin, the Stonewall Formation contains the youngest *Calapoecia* and the oldest *Propora.* All the colonial rugosans are fasciculate (*Palaeophyllum* and *Tryplasma*). The Stonewall assemblage has some similarities with the Edgewood Assemblage and with the Ellis Bay–lowermost Becscie assemblage.

On the basis of conodont biostratigraphy, Sweet (1979, p. 54, fig. 4; 1984, p. 33) concluded that uppermost strata of the Bighorn Group in Wyoming, which are probably equivalent to beds in the lower Stonewall Formation, are of post-Richmondian Ordovician age (*i.e.,* Gamachian). The position of the Ordovician–Silurian boundary in the Williston Basin is uncertain, but has been placed at the top of the Stonewall (Stearn, 1956, pp. 14–16) and at the *t* marker bed within the formation (Brindle, 1960, pp. 18, 19). On the basis of sequence stratigraphy and sea-level curves, the upper Stonewall and overlying lower Fisher Branch Formation were assigned to the Rhuddanian by Johnson and Lescinsky (1986, fig. 6). We consider the Stonewall coral assemblage to be consistent with an age assignment of Gamachian, or possibly latest Richmondian, to earliest Rhuddanian, and with an interpretation that the latest Ordovician to earliest Silurian sequence in the Williston Basin lacks significant hiatuses.

SILURIAN ASSEMBLAGE

Colonial corals are uncommon in strata immediately above those containing the Edgewood Assemblage in the east-central United States. The Silurian assemblage found in these overlying rocks is composed of the same three genera that are dominant in the Edgewood: *Paleofavosites, Propora,* and *Halysites.* We infer that at least some of the characteristic species were likely derived from Edgewood forms. For example, *Paleofavosites* sp. cf. *P. subelongus* probably arose from *P. subelongus* through the appearance of rare mid-wall pores. *Halysites* sp. cf. *H. alexandricus,* in which tabulae are commonly strongly concave, could have descended from *H. alexandricus,* which has flat to slightly concave or convex tabulae. Some species in the Silurian assemblage may have been introduced from elsewhere, or perhaps were derived from forms in other areas. For example, *Paleofavosites* sp. cf. *P. ivanovi* is comparable to *P. ivanovi* in the Upper Ordovician of the Urals and Siberian Platform (see *Discussion,* p. 95).

The change from colonial corals of the Edgewood Assemblage to those of the Silurian assemblage is generally abrupt (see Text-fig. 8, foldout inside back cover). It usually occurs between formations, at a distinct unconformity or contact that could represent a hiatus. In northwestern Illinois, however, the changeover occurs within the Mosalem Formation, and the record of the critical time interval may be most complete. The only known overlap of Edgewood and Silurian species occurs in this area, at Section 32 (Thomson East) (see

Text-fig. 7). There, Edgewood colonial and solitary corals occur in the fill of small, local channels (Section-interval 32-1b) and in strata lateral to the channels (including the coral-rich bed, Section-interval 32-1z) (see also McAuley and Elias, 1990, p. 22; Elias, 1992, p. 120). Above the filled channels (Section-interval 32-1c), *Paleofavosites* sp. cf. *P. subelongus* and all solitary rugosans represent the Silurian assemblage. Two other species in that interval also occur in the Edgewood Assemblage. *Propora thebesensis* is known to range as high as 1.35 m above the base of the interval, and *Propora speciosa* was found 0.7 m above the base. The coral-rich bed and channels suggest a period of nondeposition and local erosion, possibly recording a minor regressive event (see McAuley and Elias, 1990, p. 23; Elias, 1992, p. 120). This occurred during the worldwide transgression in the earliest Silurian (Early Llandovery, Rhuddanian), which was related to deglaciation (see Johnson *et el.,* 1985, fig. 5, eastern Iowa).

The changeover from Edgewood to Silurian assemblages took place as water depth and temperature were generally increasing during the Early Llandovery (McAuley and Elias, 1990, p. 29; Elias, 1989, p. 325). Nevertheless, corals representing the Silurian assemblage appear above local channels within the Mosalem Formation and above unconformities or formational boundaries elsewhere, suggesting that the faunal change followed a regressive event. We infer that as areas in the east-central United States became inhospitable, geographic ranges of Edgewood corals were reduced. Most species became extinct; some colonial corals apparently underwent rapid evolution, probably in small populations. The descendants dispersed and new immigrants arrived as suitable habitat areas expanded when the Early Llandovery transgression resumed. A few Edgewood colonial species evidently survived briefly in local refugia. It is noteworthy that, unlike the colonial corals, all solitary rugosans known from the Silurian assemblage are immigrants that represent genera different from those in the Edgewood Assemblage (McAuley and Elias, 1990, table 1; Elias, 1992, p. 120). Corals of the Silurian assemblage probably favored somewhat deeper, possibly warmer water than those of the Edgewood Assemblage.

THE EDGEWOOD COLONIAL CORALS: TAPHONOMY AND PALEOECOLOGY

Introduction

In this section, we examine the taphonomy and paleoecology of colonial corals in the Edgewood Assemblage, and their relationship to paleoenvironmental factors. Corallum abrasion and orientation are shown to reflect the energy level. The development of composite coralla is related to substrate stability. Encrusting corals, as well as encrusters on and borings within coralla, provide records of interactions among species. Encrusting relationships are used as indicators of substrate availability and stability, sedimentation rate, and turbidity. Corallum growth forms and growth rates are related to sedimentation rate and substrate stability; corallum size may reflect environmental stability. We conclude this section with an overview of paleoenvironments inhabited by colonial corals in the Edgewood Province, and a synthesis providing detailed paleoenvironmental determinations for stratigraphic units and localities, based on comparative taphonomy and paleoecology.

Abrasion

Abrasion of colonial coralla has rarely been considered in a paleoenvironmental context (Young, 1988, pp. 24, 25). As demonstrated for solitary rugosans (Elias *et al.,* 1988, pp. 23, 24), the degree of abrasion reflects the intensity and duration of abrasive processes. It therefore provides an indication of the energy level and sedimentation rate before final burial.

In this study, Edgewood colonial coralla are categorized as nonabraded or abraded based on examinations of their exterior surfaces in thin sections. Specimens selected for this analysis are nonweathered, well preserved, enclosed in matrix, and lack obvious stylolitized boundaries. We consider coralla to have been abraded prior to final burial if their bases are absent (Pl. 3, figs. 4, 8) and/or if calices are clearly reduced or removed completely from some or all of the upper surfaces (Pl. 14, fig. 10, Pl. 16, fig. 12); this is particularly obvious if tabulae or dissepiments are truncated. Samples of sufficient size for comparative purposes are obtained by combining data from all suitable massive tabulates in each of five collections (Table 3); these represent the orders Favositida Wedekind and Heliolitida Frech. The proportion of abraded coralla in any collection does not appear to differ between the two numerically important species, *Paleofavosites subelongus* and *Propora thebesensis.*

In the Edgewood Province, we observe minimal damage due to abrasion only in specimens from the coral-rich bedding surface in the Mosalem Formation at Section 32 (Thomson East). The proportion of abraded coralla is low in this bed (Table 3). The mudstone to wackestone lithology suggests low energy conditions.

All or the vast majority of specimens are abraded in the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry), the Leemon Formation

Table 3.—Conditions, orientations, and types of tabulate coralla in selected units within the Edgewood Province. Coralla with axes of growth within 20° of vertical are considered to be in growth orientation; those with axes more than 20° from vertical are considered to be overturned. Composite coralla show one or more marked changes in direction of growth; noncomposite coralla do not.

units	*conditions (massive coralla)*		*orientations (massive coralla)*		*types of coralla*	
section-intervals	*nonabraded*	*abraded*	*growth*	*overturned*	*noncomposite*	*composite*
Keel Fm., *Brevilamnulella* beds						
23-2	1 (7%)	13 (93%)	3 (19%)	13 (81%)	29 (100%)	0 (0%)
Keel Fm., oölite						
23-2a, 23-3, and 23a-1	–	–	–	–	14 (88%)	2 (12%)
Leemon Fm.						
31-1 and 31-1b	1 (5%)	18 (95%)	–	–	23 (82%)	5 (18%)
Bryant Knob Fm., Kissenger Lst. Mbr.						
14-1	3 (9%)	32 (91%)	5 (21%)	19 (79%)	73 (99%)	1 (1%)
15-1	0 (0%)	14 (100%)	–	–	33 (100%)	0 (0%)
Mosalem Fm., coral-rich bedding surface						
32-1z	9 (82%)	2 (18%)	8 (44%)	10 (56%)	53 (100%)	0 (0%)

at Section 31 (Thebes North), and the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm) and Section 15 (Calumet) (Table 3). The amount of damage to individual coralla appears to be greatest at Section 31, followed by Sections 14 and 15. The packstone to grainstone lithologies of all these units suggest higher energy conditions than at Section 32 (Thomson East). The proportions of nonabraded and abraded coralla at Section 32 and Section 14 are significantly different ($\chi^2 = 19.644$; $\chi^2_{0.05} = 3.841$, 1 d.f.). It appears that massive tabulate coralla in the Edgewood Province became abraded in all but the lowest energy environments.

ORIENTATION

Attitudinal disorientation of objects such as colonial corals and stromatoporoids is most likely to have resulted from toppling or transportation by wave and current energy (Jackson, 1983, p. 86; Kershaw, 1984, pp. 125–127; Harrington, 1987, pp. 660, 661). A number of other mechanisms have also been proposed, including buckling as a result of pressures within reefs (Manten, 1971, p. 435), bioturbation and predation (Kershaw, 1984, p. 125), weakening of cemented bases by boring, and substrate instability caused by growth (Kobluk *et al.*, 1977, p. 2229). There are diagnostic features that allow recognition of possible occurrences of most of these mechanisms; the absence of such features allows us to examine the relationship between orientation and environmental energy. We use data from massive Edgewood tabulates in our analyses; these represent the families Favositidae Dana and Proporidae Sokolov. None of the specimens is attached to an object large enough to have affected orientation, and all these corals inhabited unlithified substrates.

Where possible, attitudinal orientations of Edgewood colonial coralla with respect to bedding were marked in the field and confirmed later using thin sections. Because the data set is small, we recognize just two classes; those in growth orientation and those that are overturned (disoriented). Coralla in which the growth direction differs by more than 20° from upright are considered to be overturned. We follow Philcox (1971, p. 344) in distinguishing the terms "growth orientation" and "growth location."

Most coralla are overturned in each of the three collections from which sufficient data are available for comparison (Table 3). Although attitudinal orientations do not differ significantly between the intervals (χ^2 tests), it is noteworthy that a smaller proportion is overturned on the coral-rich bedding surface of the Mosalem Formation at Section 32 (Thomson East) than in the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry) or the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm). That might be expected considering the lower energy conditions indicated by the mudstone to wackestone lithology and high proportion of nonabraded coralla at Section 32, compared with the packstone to grainstone lithologies and high proportions of abraded coralla at the other sections.

It must be remembered, however, that differences in attitudinal orientations between collections do not *necessarily* indicate different environmental energies. Simple comparisons ignore important variables such as skeletal density, size, growth form, and substrate morphology and consistency (see Kershaw, 1984, pp. 125–127). The problem of density can be overcome by limiting analyses to coralla of comparable structure.

Table 4.—Orientations of massive Edgewood tabulate coralla in various size and growth form categories. Coralla with axes of growth within 20° of vertical are considered to be in growth orientation; those with axes more than 20° from vertical are considered to be overturned.

	orientations	
categories	*growth*	*overturned*
corallum sizes		
10.5–30.0 mm	3 (19%)	13 (81%)
30.5–50.0 mm	7 (30%)	16 (70%)
50.5–70.0 mm	5 (50%)	5 (50%)
growth forms		
columnar	0 (0%)	5 (100%)
high bulbous	3 (27%)	8 (73%)
low bulbous	1 (20%)	4 (80%)
high domical	6 (35%)	11 (65%)
low domical	5 (45%)	6 (55%)

The spacing and thickness of skeletal elements in the Edgewood favositids and proporids appear to be approximately equivalent.

Little attention has been given to the relationship between corallum size and attitudinal orientation. It might be expected that, other things being equal, small coralla would be overturned more easily than large ones. In an analysis of hemispherical tabulates and stromatoporoids, Kobluk *et al.* (1977) concluded that there was no difference in the sizes of oriented and disoriented specimens, possibly because energy levels involved in the disorientation process were so high that all specimens were affected. Harrington (1987, p. 660), however, argued that the data of those authors suggest "a slight tendency toward more frequent disorientation of smaller individuals."

In the present study, attitudinal orientations are compared for three size categories of massive Edgewood tabulates (favositids and proporids), using average linear dimension (*i.e.,* (maximum width + height) ÷ 2; see *Corallum Size,* p. 32) as a measure of size (Table 4). The proportion of coralla in growth orientation increases with increased size, although there are too few specimens to confirm this statistically. Such a pattern suggests that at least some coralla in growth orientation are in fact in growth location. If all specimens had been transported, the proportion deposited in growth orientation would not be expected to differ among size classes, other things being equal.

Growth form will affect the probability of disorientation because objects such as colonial corals and stromatoporoids with lower forms are apparently less likely than tall ones to be overturned by currents or waves (Manten, 1971, p. 437; Harrington, 1987, p. 660; Kershaw, 1990, p. 699). Nevertheless, it appears from flume experiments that stromatoporoids with laminar shapes are more readily overturned than those with low domical forms (Kershaw, 1984, p. 125). Domical forms are most likely to be deposited in growth orientation following transportation because that is the most stable attitude (Abbott, 1974, p. 8), but they may also be overturned 180°. Columnar forms are most stable when disoriented 90°, with their long axes parallel to bedding (Hodges and Roth, 1986, p. 1153).

We compare attitudinal orientations of massive Edgewood tabulates (favositids and proporids) using five growth form categories (see *Growth Form,* pp. 27, 28) (Table 4). All columnar coralla are overturned. Proportions of coralla in growth orientation are intermediate for high and low bulbous forms and high domical forms. As expected, the proportion in growth orientation is highest for low domical coralla, although there are too few specimens to confirm these patterns statistically.

The possible effects of corallum size and growth form on attitudinal orientation should be taken into account when comparing data from different localities or units for the purpose of inferring environmental energy levels. We therefore recommend that comparisons be done within the classes of a standardized set of size groupings for each growth form category. Unfortunately, there are insufficient data to conduct such an analysis in the Edgewood Province.

Substrate morphology is an important variable in orientation analysis because of its relationship to the stability and mobility of objects such as corals and stromatoporoids (Kershaw, 1984, p. 125). Movement can be inhibited if coralla are closely spaced. That may account in part for the comparatively high proportion of specimens in growth orientation on the coral-rich bedding surface at Section 32 (Thomson East). Overturned domical forms are more likely to be preserved in an inverted position, rather than be reoriented into the more stable growth orientation, if lodged against other objects (Abbott, 1974, p. 12). Overturned coralla in contact with other specimens were observed on the coral-rich bedding surface at Section 32. The effects of substrate stability on coral orientation are considered under *Composite Coralla,* below.

COMPOSITE CORALLA

In this study, use of the term "composite" follows Young and Scrutton (1991, p. 371); it is restricted to coralla that show one or more marked changes in the direction of growth, as observed in longitudinal section (*e.g.,* Pl. 5, fig. 8). Philcox (1971, p. 341) used the term in a broader sense, including coralla in which regeneration was not accompanied by changes in growth direction. Redirected growth records a change in orientation during the life of the colony (Jackson, 1983, p. 86); the event causing disorientation was not severe enough to effect mortality by abrasion, burial, or transportation. Scouring of the sediment supporting unattached coralla could result in decreased stability and in overturning, leading to the development of composite forms. The ease with which sediment can be eroded is related to its cohesion. Sand is typically less cohesive than mud and can be eroded at relatively low current velocities (Potter *et al.*, 1980, p. 11); it therefore generally forms a less stable substrate.

Data from representatives of the orders Favositida, Heliolitida, and Halysitida Sokolov in the Edgewood Province (Table 3) support the interpretation that formation of composite coralla is related to substrate stability. Composite specimens are most common in the Leemon Formation at Section 31 (Thebes North) and in oölites of the Keel Formation at Section 23 (Lawrence Quarry). Lithologies at both localities suggest sandy sediments of low cohesion. Coralla from Section 31 are in a skeletal grainstone with moderately well-rounded grains (see Amsden, 1986, pl. 1, fig. 2), and those from Section 23 are in an oölitic grainstone (see Amsden, 1960, pl. 10, figs. 5, 6; 1986, pl. 6, fig. 1).

The proportion of composite coralla in the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm) is significantly lower than that in the Leemon Formation at Section 31 (Thebes North) ($\chi^2 = 7.237$; $\chi^2_{0.05} = 3.841$, 1 d.f.). The pronounced alignment of clasts in the fossiliferous grainstone at Section 14 may have resulted in greater substrate stability. Composite specimens are absent in grainstone of the Kissenger Limestone at Section 15 (Calumet); this is significantly different from the proportion at Section 31 ($\chi^2 = 4.265$; $\chi^2_{0.05} = 3.841$, 1 d.f.). Composite coralla are also absent in the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry). The alignment of brachiopod shells in that oölitic, bioclastic packstone to grainstone may have increased substrate stability (see Amsden, 1986, pl. 2, fig. 1, pl. 3, fig. 2). The absence of composite colonies on the coral-rich bedding surface of the Mosalem Formation at Section 32 (Thomson East) is significantly different from Section 31 ($\chi^2 = 7.239$; $\chi^2_{0.05} = 3.841$, 1 d.f.). The mudstone to wackestone lithology at Section 32 suggests that sediment cohesion was relatively high.

ENCRUSTING RELATIONSHIPS

Analysis of encrusting relationships involving colonial corals provides information about the duration of exposure of skeletal material. This is useful in determining environmental factors such as sedimentation rate and substrate availability and stability. Such analysis also sheds light on the paleobiology of corals and other encrusters, and on interactions among species.

In this study, the term "encruster" is applied to all organisms that grew initially on hard substrates, even if most subsequent growth was vertical. It is not restricted to those having primarily laminar or runner forms (*cf.*, Taylor, 1990, pp. 346, 347). Examinations of thin sections reveals that Edgewood colonial corals were involved in a variety of encrusting relationships. They were both substrates for encrusting organisms including other corals, and active encrusters of coralla and other objects.

Coatings of micritic, thrombolitic, and rarely *Girvanella*-like forms, presumed to be of algal origin, are the most common type of encrustation on Edgewood colonial coralla. We have observed them on *Propora thebesensis, Protaraea* sp. A, *Halysites alexandricus, Paleofavosites subelongus,* and *Palaeophyllum* sp. Such coatings generally cover a large portion of the corallum surface, which was usually abraded prior to encrustation. The algae do not seem to have been host-specific, and evidently became associated with coralla during or following post-mortem transport (see also McAuley and Elias, 1990, p. 30). Algal-coated specimens are widely distributed in the Edgewood Province, but the proportion of colonial coralla with such encrustations is greatest in the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry) (Table 5).

Edgewood colonial coralla having attached animals are relatively common only in the *Brevilamnulella* beds and oölites of the Keel Formation at Section 23 (Lawrence Quarry) (Table 5). The most common encrusting animals are bryozoans, which are usually laminar in form and small. One bryozoan colony occurs on a specimen of *Palaeophyllum* sp. from the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm) (Pl. 21, figs. 10–12), but all other bryozoans occur on *Halysites alexandricus.* We observed them on four coralla from the *Brevilamnulella* beds at Section 23, one from the Keel oölite at Section 23, one from the upper oölitic bed of the Keel at Section 24 (Coal Creek), and two from the Kissenger Limestone at Section 15 (Calumet).

Encrusting stromatoporoids have been observed on single coralla of *Propora thebesensis* (above an algal coating), *Protaraea* sp. A, and *Paleofavosites subelongus* from the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry), and on single specimens of *P. subelongus* from the Keel oölite at Section 23 and the unnamed member of the Bryant Knob Formation at Section 18 (Kissenger). A small, unidentifiable solitary rugosan occurs on a specimen of *Halysites alexandricus* from the *Brevilamnulella* beds

Table 5.—Encrusting relationships involving colonial corals in selected units within the Edgewood Province.

units *section-intervals (n = no. of coralla)*	*colonial coralla with encrusters* *algal*	*animal*	*all types*	*encrusting colonial corals*
Keel Fm., *Brevilamnulella* beds				
23-2 (n = 29)	11 (38%)	8 (28%)	17 (59%)	7 (24%)
Keel Fm., oölite				
23-2a, 23-3, and 23a-1 (n = 11)	2 (18%)	3 (27%)	5 (45%)	1 (9%)
Leemon Fm.				
31-1 and 31-1b (n = 19)	0 (0%)	1 (5%)	1 (5%)	0 (0%)
Bryant Knob Fm., Kissenger Lst. Mbr.				
14-1 and 14-2 (n = 31)	4 (13%)	1 (3%)	4 (13%)	0 (0%)
15-1 (n = 23)	2 (9%)	2 (9%)	4 (17%)	0 (0%)
Mosalem Fm., coral-rich bedding surface				
32-1z (n = 45)	2 (4%)	0 (0%)	2 (4%)	0 (0%)

at Section 23. One corallum of the solitary rugosan *Keelophyllum oklahomense* McAuley and Elias from the Keel oölite at Section 23 is attached to *H. alexandricus* (in part above a thin encruster that is probably a bryozoan) (McAuley and Elias, 1990, pl. 12, fig. 4; Pl. 9, fig. 9). A probable tentaculitid occurs on a specimen of *H. alexandricus* from the Leemon Formation at Section 31 (Thebes North) (Pl. 10, fig. 4).

Encrusting colonial corals are relatively common in the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry) (Table 5). *Protaraea* sp. A, which is restricted to those beds, typically has a small, thin, tabular form. One specimen was observed to encrust both *Halysites alexandricus* (Pl. 8, fig. 12) and *Aulopora* sp. A, and another occurs on a stromatoporoid. One corallum of the large cateniform species *H. alexandricus* is attached to both *Protaraea* sp. A and a stromatoporoid (Pl. 9, fig. 8), and another encrusts the solitary rugosan *Streptelasma leemonense* Elias. Two specimens of the small cateniform species *Catenipora lawrencica* occur on *H. alexandricus*, and one of them is also attached to *S. leemonense*. *Aulopora* sp. A is a small coral with an irregular, low, reptant form. One example encrusts *H. alexandricus*, a stromatoporoid, and calcareous algae (Pl. 20, fig. 1).

Encrusting colonial corals are rare or absent elsewhere in the Edgewood Province (*e.g.*, Table 5). Single examples of *Paleofavosites subelongus* on stromatoporoids are known from the Keel oölite at Section 23 (Lawrence Quarry) and the unnamed member of the Bryant Knob Formation at Section 18 (Kissenger). One specimen of *P. subelongus* occurs on an algal crust in the Kissenger Limestone Member of the Bryant Knob (Section-interval 18-2). *Protaraea* sp. A, *Catenipora lawrencica*, and *Aulopora* sp. A are the only Edgewood colonial corals that seem to have been primarily encrusters. *Halysites alexandricus* and *P. subelongus* rarely had encrusting modes of life.

Most of the encrusting animals that colonized colonial coralla appear to have favored the lateral and upper surfaces of ranks in *Halysites alexandricus* as a substrate. This was probably because lacunae within the cateniform skeleton provided protected sites for colonization and the available surface area was high. One corallum of *H. alexandricus* from the *Brevilamnulella* beds at Section 23 (Lawrence Quarry) is encrusted in different places by a bryozoan, *Catenipora lawrencica*, *Aulopora* sp. A, and a solitary rugosan. Another is encrusted in different places by a bryozoan, *Protaraea* sp. A, and *C. lawrencica*. In most cases, animals attached to colonial coralla as well as encrusting colonial corals evidently grew on skeletons of dead hosts. Where multiple encrustation of the same substrate occurred, as in the *Brevilamnulella* beds of the Keel Formation at Section 23, there is generally evidence of reorientation and abrasion between colonization events.

In the Edgewood Province, colonial coralla with encrustations of all types are common only in the *Brevilamnulella* beds and oölitic beds of the Keel Formation at Section 23 (Lawrence Quarry) (Table 5). The proportion of encrusted coralla is significantly greater in the *Brevilamnulella* beds than in the Leemon Formation at Section 31 (Thebes North), the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm) and at Section 15 (Calumet), and the coral-rich bedding surface of the Mosalem Formation at Section 32 (Thomson East) ($\chi^2 = 11.760, 11.829, 7.425$, and 24.359, respectively; $\chi^2_{0.05} = 3.841$, 1 d.f.). Encrusting colonial corals are common only in the *Brevilamnulella* beds (Table 5). These patterns seem to reflect predictable limiting factors in the distribution of encrusters: substrate availability and stability, sedimentation rate, and turbidity.

Skeletal objects including relatively large colonial coralla that could have served as attachment sites for encrusters are abundant in the *Brevilamnulella* beds, which in places are coquinoid (see Amsden, 1986, p. 10). The aligned brachiopod shells and absence of composite colonial corals suggest a stable substrate favorable for attachment and subsequent growth. A low sedimentation rate would have provided sufficient time for numerous objects to become encrusted, and for multiple encrustation of some coralla. We describe the *Brevilamnulella* beds as "incipient biohermal." It seems that periodic overturning of coralla, perhaps during occasional storms, inhibited the development of complex, long-term encrusting relationships that could have led to the formation of bioherms. The lithology and relatively high frequency of composite coralla in the less fossiliferous Keel oölite suggest lower substrate availability and stability; the observed frequency of encrusted coralla is higher than might be expected. At least some of those coralla may have been transported from the *Brevilamnulella* beds.

The rarity of encrusting relationships in the Leemon Formation at Section 31 (Thebes North), where the frequency of composite corals is greatest, can be attributed to substrate instability and possibly also to a relatively high sedimentation rate. Encrusted colonial coralla are uncommon in the Kissenger Limestone Member of the Bryant Knob Formation. The alignment of clasts and rarity of composite coralla at Section 14 (Higginbotham Farm), and the absence of composite coralla at Section 15 (Calumet), suggest that substrate stability was comparatively high. Perhaps encrusters were hindered by relatively high sedimentation rates at those localities. Encrusting relationships are rare in the Mosalem Formation at Section 32 (Thomson East), where the mudstone to wackestone lithology suggests that encrusters may have been inhibited by turbid conditions.

BORINGS

Borings in coral skeletons, produced by soft-bodied organisms that are not otherwise preserved, add to the record of biodiversity. Analysis can reveal whether boring occurred during life or after death of the host. This provides information about the paleobiology of both the coral and the endolith.

In our examinations of Edgewood colonial coralla, we observed borings only in a single specimen of *Protaraea* sp. A from the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry). Microborings are abundant in thin sections of that corallum (Pl. 8, figs. 8–11). They are tubular, slightly curved or less commonly straight, and in some cases have randomly located low-angle bends. Branches may arise at irregular intervals and may be oriented at various angles. Bulbous enlargements of variable shape occur along some borings. Diameters of the tubular borings are generally 25 to 75 μm, but the largest tubular borings and bulbous enlargements are 400 μm across. Diameter may vary along the length of a boring. The maximum observed length is 3.75 mm. Terminations of tubular borings are rounded.

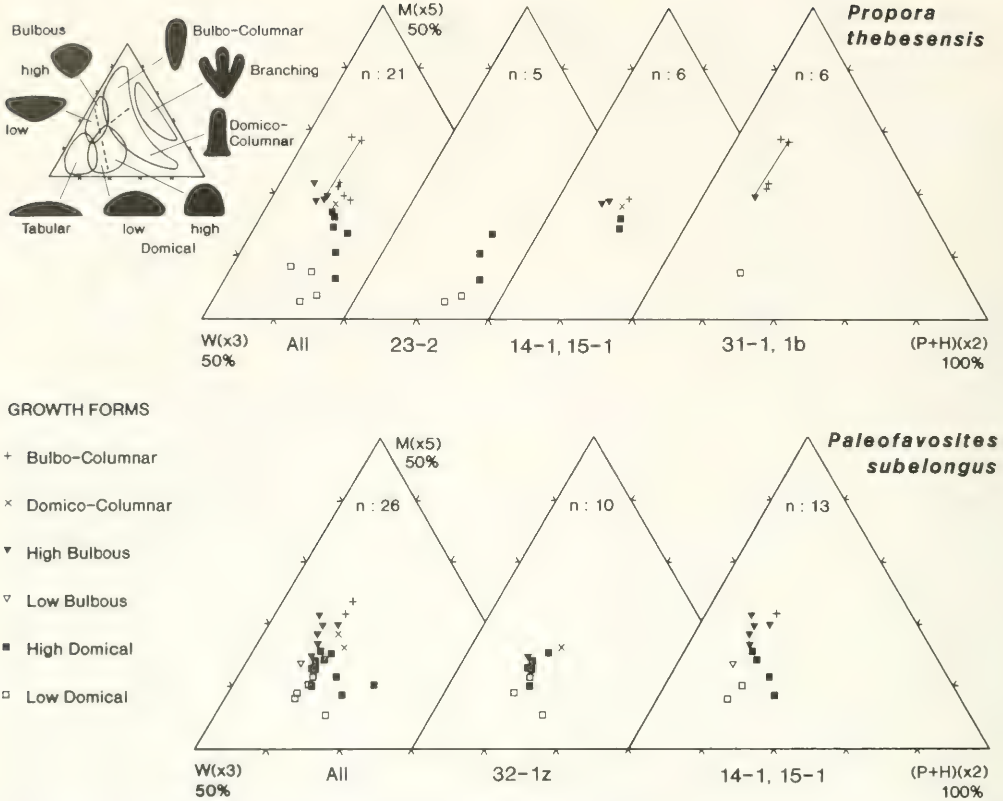
The smaller borings are filled with micritic material. Larger ones may be filled with micrite or more commonly have only a micritic lining, but micrite is absent in a few of the largest. Some of the borings penetrate into the calical and basal surfaces of the corallum. Most are located in the interior of the skeleton, where some penetrate upward or downward from regeneration surfaces, or follow along or cross such surfaces. There is a tendency for tubular borings to parallel trabeculae of the coral skeleton.

The morphology and size of these microborings are comparable to some of those in a Middle Ordovician stromatoporoid from Norway, documented by Pickerill and Harland (1984, figs. 3b, 3d). Such structures are considered to be of probable sponge origin (Pickerill and Harland, 1984, p. 889). *Protaraea* sp. A has the densest skeleton of any Edgewood coral. It is virtually solid, forming an ideal substrate for borers. The distribution and orientation of borings suggest that the corallum surface was colonized by endoliths between regeneration events, as well as following death of the coral and transportation of the skeleton.

GROWTH FORM

Based on our study of Edgewood tabulates, we are able to expand and refine the quantitative methods for analysis of colonial coral growth forms that were established by Young and Scrutton (1991). This permits detailed examination of ranges of variation, and comparison of subtle differences in form within and among stratigraphic units and localities. Various aspects of corallum growth form are related to sedimentation rate and substrate stability.

To document the growth forms of Edgewood tabulate coralla, lateral profiles of nonabraded or slightly abraded specimens are produced. Most coralla are enclosed in matrix; outlines of these are taken from polished longitudinal surfaces or from thin sections through the corallum growth axis. The following parameters are measured: corallum width (W), height (H), height to the widest point (M), and, if possible, perimeter (P) (see Young and Scrutton, 1991, p. 372, fig. 2a). Growth forms of coralla are defined using the system of Young and Scrutton (1991, pp. 370, 371). The categories include tabular ($W{:}H \geq 3{:}1$, base and upper surface subparallel; some coralla of *Protaraea* sp. A have this form), domical ($W{:}H \geq 1{:}1$ but $< 3{:}1$, $M < 0.5H$), bulbous ($W{:}H \geq 1{:}1$ but $< 3{:}1$, $M \geq 0.5H$), columnar



Text-figure 10.—Triangle diagrams showing growth forms of *Propora thebesensis* (top row) and *Paleofavosites subelongus* (bottom row). W = corallum width, H = corallum height, M = height to the widest point, P = corallum perimeter; the three values plotted are W (× 3) (range 0–50%), M (× 5) (range 0–50%), and (P + H) (× 2) (range 50–100%). Percentages are of the total for the three plotted values. For example, a corallum having W = 100 mm, H = 50 mm, M = 40 mm, and P = 250 mm would have values of W (× 3) = 300 (27.3%), M (× 5) = 200 (18.2%), and (P + H) (× 2) = 600 (54.5%); such a specimen would plot in the lower left part of the field for low bulbous growth forms shown in the small standard triangle diagram in the upper left of the text-figure. For each species, the plot for all measurable coralla from the east-central United States is identified; other plots are for the Section-intervals indicated; n = number of coralla (two parts of one composite corallum were considered separately). Each data point represents a single corallum, except where a solid line connects points from a composite corallum; symbols for growth forms are listed in the lower left of the text-figure. The small standard triangle diagram shows fields in which various growth form categories plot; lateral profiles of representative coralla are shown as silhouettes.

(W:H < 1:1, sides subparallel), and branching (*i.e.*, dendroid or digitate; no Edgewood coralla have this form). In addition, we subdivide columnar forms into two categories, domico-columnar (M < 0.5H) and bulbo-columnar (M ≥ 0.5H). We also define low and high categories for both domical and bulbous coralla by bisecting the field for those forms on graphs of corallum width *versus* height (*i.e.*, low, W:H ≥ 1.6:1 but < 3:1; high, W:H ≥ 1:1 but < 1.6:1).

Growth forms of specimens of *Propora thebesensis* and *Paleofavosites subelongus* for which the necessary parameters can be measured are plotted on triangle diagrams using the techniques of Young and Scrutton (1991, p. 373, fig. 3) (Text-fig. 10). Such diagrams permit graphical depiction of ranges of variation and subtle differences in form. Both species show similar degrees of variation, and both include domical, bulbous, and columnar coralla, but patterns of variation are not identical. Triangle diagrams for Section-interval 14-1 (Higginbotham Farm) and Section-interval 15-1 (Cal-

Table 6.—Corallum growth forms of selected tabulate species in units within the Edgewood Province.

units *section-intervals* *species (n = no. of coralla)*	*bulbous forms*			*domical forms*		
	bulbo-columnar	*high bulbous*	*low bulbous*	*domico-columnar*	*high domical*	*low domical*
Keel Fm., *Brevilamnulella* beds						
23-2						
Propora thebesensis (n = 6)	0 (0%)	0 (0%)	1 (17%)	0 (0%)	3 (50%)	2 (33%)
		1 (17%)			5 (83%)	
Leemon Fm.						
31-1 and 31-1b						
Propora thebesensis (n = 10[1])	7 (70%)	1 (10%)	0 (0%)	0 (0%)	0 (0%)	2 (20%)
		8 (80%)			2 (20%)	
Bryant Knob Fm., Kissenger Lst. Mbr.						
14-1						
Propora thebesensis (n = 10)	2 (20%)	3 (30%)	2 (20%)	1 (10%)	2 (20%)	0 (0%)
		7 (70%)			3 (30%)	
Paleofavosites subelongus (n = 24)	2 (8%)	7 (29%)	3 (13%)	0 (0%)	6 (25%)	6 (25%)
		12 (50%)			12 (50%)	
15-1						
Propora thebesensis (n = 4)	0 (0%)	3 (75%)	0 (0%)	0 (0%)	1 (25%)	0 (0%)
		3 (75%)			1 (25%)	
Paleofavosites subelongus (n = 4)	0 (0%)	2 (50%)	1 (25%)	0 (0%)	0 (0%)	1 (25%)
		3 (75%)			1 (25%)	
Mosalem Fm., coral-rich bedding surface						
32-1z						
Paleofavosites subelongus (n = 23)	0 (0%)	2 (9%)	1 (4%)	1 (4%)	11 (48%)	8 (35%)
		3 (13%)			20 (87%)	

[1] Includes two parts of one composite corallum that are considered separately.

umet), in which both species occur, indicate that *P. subelongus* was more likely to develop low domical forms than was *P. thebesensis.* This corresponds with observed differences in basal astogeny. Corallites tended to diverge widely from the point of initiation in *P. subelongus,* producing flatter corallum bases (Pl. 16, fig. 5), whereas corallites of *P. thebesensis* diverged less broadly and corallum bases are usually more conical (Pl. 3, figs. 4, 8). It is because of these interspecific differences that comparisons of growth form distribution between collection intervals are made within species.

There are substantial differences in growth form among stratigraphic units (Text-fig. 10; Table 6). Domical coralla of *Propora thebesensis* having relatively flat basal surfaces (*i.e.,* $M \ll 0.5H$) are dominant in the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry). In the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm) and Section 15 (Calumet), coralla of *P. thebesensis* are domical or bulbous and plot near the boundary between those categories (*i.e.,* M nearly 0.5H). Bulbo-columnar specimens of *P. thebesensis,* some with steeply conical bases (*i.e.,* $M \gg 0.5H$), are dominant in the Leemon Formation at Section 31 (Thebes North). In *Paleofavosites subelongus,* domical coralla having somewhat conical bases (*i.e.,* M approaching 0.5H) are dominant on the coral-rich bedding surface of the Mosalem Formation at Section 32 (Thomson East). Domical and bulbous forms are common for *P. subelongus* from Sections 14 and 15.

Within a species, variation in shapes of corallum bases may reflect differences in sedimentation rate and/or sediment firmness during growth (see Philcox, 1971, p. 340; Gibson and Broadhead, 1989, pp. 294–295). If sediment did not accumulate around a corallum, and if it was sufficiently firm to provide a stable substrate that prevented subsidence as weight of the skeleton increased during growth, then a flat basal surface would have developed during colony expansion over a level bottom. The greater the rate of sediment accumulation and/or corallum subsidence, the more steeply conical the base would become (*i.e.,* the greater the M:H ratio, other things being equal). The proportions of domical and bulbous coralla of a species may therefore reflect the sedimentation rate and substrate stability.

Table 7.—Growth forms and spacing of tabulae and dissepiments (where applicable) in selected tabulate coralla from the Edgewood Province. *High* = high bulbous and/or high domical, *low* = low bulbous and/or low domical, *n* = number of coralla, range and standard deviation (*s.d.*) are for corallum means.

species *units* *section-intervals*	*growth forms*				*no. of tabulae in 5 mm*				*no. of dissepiments in 5 mm*			
	columnar	*high*	*low*	*n*	*mean*	*range*	*s.d.*	*n*	*mean*	*range*	*s.d.*	*n*
Propora thebesensis												
Keel Fm., *Brevilamnulella* beds												
23-2	0 (0%)	3 (50%)	3 (50%)	4	9.2	6.2–13.3	2.0	10	17.5	11.9–20.0	3.8	4
Leemon Fm.												
31-1 and 31-1b	7 (70%)	1 (10%)	2 (20%)	10[1]	6.7	4.4–8.2	1.1	12	13.0	10.6–17.0	2.3	6
Bryant Knob Fm., Kissenger Lst. Mbr.												
14-1	3 (30%)	5 (50%)	2 (20%)	10	7.1	5.0–11.2	1.7	18	13.9	11.4–15.8	1.4	11
15-1	0 (0%)	4 (100%)	0 (0%)	4	7.9	4.6–9.6	1.6	11	14.0	12.8–14.9	0.9	4
Paleofavosites subelongus												
Leemon Fm.												
31-1 and 31-1b	0 (0%)	0 (0%)	1 (100%)	1	3.8	3.1–4.8	0.8	4	—	—	—	—
Bryant Knob Fm., Kissenger Lst. Mbr.												
14-1	2 (8%)	13 (54%)	9 (38%)	24	4.8	2.8–6.7	1.1	32	—	—	—	—
15-1	0 (0%)	2 (50%)	2 (50%)	4	5.8	3.5–10.9	2.6	6	—	—	—	—
Mosalem Fm., coral-rich bedding surface												
32-1z	1 (4%)	13 (57%)	9 (39%)	23	3.7	2.5–5.8	0.7	17	—	—	—	—

[1] Includes two parts of one composite corallum that are considered separately.

Another aspect of corallum form that may reflect sedimentation rate and/or substrate stability is the height : width ratio. Tall colonies are thought to shed sediment more readily than lower ones (*e.g.*, Manten, 1971, p. 431; Pandolfi, 1984, p. 540; Young and Scrutton, 1991, pp. 380, 381), although form must have combined with polyp morphology and behavior to keep surfaces sediment-free (Hubbard and Pocock, 1972; Bak and Elgershuizen, 1976; Lasker, 1980). Colony growth may have been directed preferentially upward in order to compensate for sediment accumulation (see Young and Scrutton, 1991, p. 381) or corallum subsidence. The greater the rate of sediment accumulation and/or corallum subsidence, the higher the height:width ratio would have become (other things being equal). The proportions of low, high, and columnar coralla may therefore reflect the sedimentation rate and substrate stability.

A high overall frequency of low domical forms of *Propora thebesensis* occurs in the *Brevilamnulella* beds (Text-fig. 10; Tables 6, 7), suggesting a stable substrate and low sedimentation rate. This is consistent with interpretations based on the presence of aligned shells in the sediment, the absence of composite coralla, and the high proportions of encrusted and encrusting colonial coralla. The occurrence of taller domical and bulbous forms of *P. thebesensis* in the Kissenger Limestone at Section 14 (Higginbotham Farm) and Section 15 (Calumet) suggests that the substrates were less stable and/or that sedimentation rates were higher. It is more likely that the latter was the case, since the low proportion of encrusted coralla and absence of encrusting coralla are consistent with the interpretation that sedimentation rates were high, and aligned clasts in the sediment at Section 14 and the low proportion of composite coralla suggest stable substrates. The predominantly bulbo-columnar coralla of *P. thebesensis* in the Leemon Formation at Section 31 (Thebes North) suggest a high sedimentation rate and/or unstable substrate. That both factors were involved is indicated by the well-rounded grains comprising the sediment, the high proportion of composite coralla, low proportion of encrusted coralla, and absence of encrusting coralla.

For *Paleofavosites subelongus*, the highest frequency of domical coralla is observed on the coral-rich bedding surface of the Mosalem Formation (Text-fig. 10; Table 6). The inference that the substrate was stable is consistent with the high sediment cohesion suggested by the mudstone to wackestone lithology and absence of composite coralla. The inferred low sedimentation rate is consistent with the interpretation that a break in sedimentation permitted colonization of the bedding surface by numerous corals. The proportions of domical and bulbous coralla of *P. subelongus* on the coral-rich bedding surface of the Mosalem differ significantly from those in the Kissenger Limestone at Section 14 (Higginbotham Farm) ($\chi^2 = 5.779$; $\chi^2_{0.05} = 3.841$, 1 d.f.). The greater frequency of bulbous coralla in the Kissenger at Section 14 and Section 15 (Calumet) is consistent with higher sedimentation rates, as discussed for *Propora thebesensis,* above.

There may be a genetic component to differences in growth form within both *Propora thebesensis* and *Paleofavosites subelongus* among the collections studied. At least some of the stratigraphic units differ slightly in age, the localities are separated by considerable distances, and internal morphology can be distinctly different between section-intervals (see *Aspects of Intraspecific Variation,* pp. 35, 39). There is a strong correlation between genotype and growth form in some modern corals (*e.g.,* Hunter, 1985; Willis and Ayre, 1985). It is probable, however, that environmental factors were more significant in determining the observed variation; the corals in these collections clearly lived under quite different environmental conditions. Sedimentation rate and substrate stability appear to have been important factors controlling the expressed forms of Edgewood colonial coralla, a conclusion also reached in studies of some other heliolitids and favositids (*e.g.,* Manten, 1971, pp. 431, 432; Philcox, 1971; Pandolfi, 1984; Gibson and Broadhead, 1989; Young and Scrutton, 1991).

GROWTH RATE

Absolute linear growth rates of Paleozoic corals are generally inferred using the widely accepted technique of measuring thicknesses of presumably annual high- and low-density couplets within the skeleton (see Scrutton, 1989, p. 37). Cyclic growth banding such as this is very subtle to unrecognizable in Edgewood colonial coralla, so we are unable to use this technique to determine growth rates. There is some evidence from tabulate corals that horizontal skeletal elements were formed at relatively uniform time intervals within corallites of a corallum and within coralla of a species, regardless of growth rate and colony form (Scrutton, 1989, p. 38; Young and Scrutton, 1991, p. 377). Comparisons of mean tabular or dissepimental spacing may therefore reveal differences in relative linear growth rates. This method yields meaningful results in our analysis of Edgewood corals; inferred relative linear growth rates can be related to environmental factors such as sedimentation rate, substrate stability, and turbidity.

As a measure of tabular or dissepimental spacing, we use the mean number of horizontal skeletal elements per 5 mm vertical interval within a corallum (see *Biometric Methods,* p. 44). The overall mean of corallum means is calculated for specimens of *Propora thebesensis* and *Paleofavosites subelongus* in collections from the Edgewood Province for which sufficient data are available to permit comparison (Table 7). Overall mean values for tabulae as well as dissepiments in *P. thebesensis* and for tabulae in *P. subelongus* increase from the Leemon Formation at Section 31 (Thebes North) to the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm) to the Kissenger at Section 15 (Calumet). Although there is considerable variability of corallum means within each collection, the consistent relationship when comparing overall means for these collections suggests that this pattern is real; thus, the two species may have responded in the same way to environmental differences among the localities. The highest values for *P. thebesensis* occur in the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry). The lowest values for *P. subelongus* are recorded from the coral-rich bedding surface in the Mosalem Formation at Section 32 (Thomson East).

Inferred relative linear growth rates of coralla are inversely proportional to values for spacing of tabulae or dissepiments (*e.g.,* a low growth rate would result in crowding of horizontal skeletal elements, giving a high value for spacing). Thus, mean coral growth rates increased from lowest in the *Brevilamnulella* beds, to the Kissenger Limestone at Section 15 (Calumet), to the Kissenger at Section 14 (Higginbotham Farm), to the Leemon Formation, to highest on the coral-rich bedding surface in the Mosalem.

In *Propora thebesensis,* growth rates correlate closely with the height : width aspect of growth form, suggesting that the two are interrelated. The collection from the *Brevilamnulella* beds at Section 23 (Lawrence Quarry) has the lowest mean growth rate and the greatest proportion of low growth forms (Table 7). The highest mean growth rate for this species is in the Leemon Formation at Section 31 (Thebes North), where the proportion of columnar forms is greatest. Growth rates in the Kissenger Limestone at Section 14 (Higginbotham Farm) and Section 15 (Calumet) are intermediate, and the distributions of growth forms are centered on the "high" category. We have related the corallum height : width ratio to sedimentation rate and substrate stability, and it follows that growth rate may also be an indicator of those environmental parameters. A greater vertical growth rate would have helped to maintain the position of the living polypal colony surface above the substrate where sedimentation and/or corallum subsidence rates were high. We recognize that other factors would also have been involved in determining growth rates; controls over coral growth are complex and in general poorly understood (see Buddemeier and Kinzie, 1976).

It is noteworthy that a similar close relationship involving growth rate, height : width aspect of growth form, and sedimentation rate has been found in another heliolitid, *Stelliporella parvistella* (Roemer) from the Silurian of northwestern Europe. Young and Scrutton (1991, pp. 377, 380, 381) concluded that growth rates in that species were greater in columnar and branching colonies, the predominant forms where sedimentation was moderate, than in tabular and domical colonies, which were dominant where sedimentation was minimal. It was found by Young and Scrutton that growth rates and forms could change within a colony in response to changes in sedimentation rate. In the Edgewood favositid *Paleofavosites subelongus*, there does not appear to be a consistent correlation between growth rate and the height : width aspect of growth form (Table 7).

The low mean growth rate inferred for corals in the *Brevilamnulella* beds suggests a low sedimentation rate and stable substrate. That is consistent with interpretations based on the presence of aligned brachiopod shells in the sediment, the absence of composite coralla, the high proportions of encrusted and encrusting colonial coralla, the high frequency of domical growth forms, and the high proportion of low forms among the domical and bulbous coralla. Higher mean growth rates for corals in the Kissenger Limestone are consistent with the interpretation that the sedimentation rate was higher, based on the low proportion of encrusted coralla, absence of encrusting coralla, dominance of bulbous coralla, and greater proportion of high and columnar forms. High mean growth rates for corals in the Leemon Formation suggest that the sedimentation rate was high and/or the substrate was unstable. The conclusion that both factors were involved is consistent with interpretations based on the roundness of grains comprising the sediment, the high proportion of composite coralla, low proportion of encrusted coralla, absence of encrusting coralla, and dominance of bulbous and columnar growth forms.

The high mean growth rate inferred for colonies on the coral-rich bedding surface in the Mosalem Formation is more difficult to interpret. It does not appear to reflect a high sedimentation rate or a substrate that was unstable. The predominance of domical coralla and high proportion of low growth forms suggest that the sedimentation rate was low and the substrate was stable. A low sedimentation rate is consistent with the interpretation that this bed represents a break in deposition. The conclusion that the substrate was stable is supported by the mudstone to wackestone lithology, suggesting high sediment cohesion, and the absence of composite coralla. Growth rates of modern corals decrease as turbidity increases (see Buddemeier and Kinzie, 1976, p. 211). Comparatively low growth rates might therefore be expected for the coral-rich bedding surface in the Mosalem, where the lithology, low proportion of coralla with encrusters, and absence of encrusting coralla are considered to reflect relatively high turbidity. In this case, it is possible that the high growth rate was related to favorable environmental conditions that permitted colonization of the bedding surface by numerous corals (*e.g.*, factors such as temperature, nutrients).

CORALLUM SIZE

Our study of Edgewood colonial corals shows that the sizes attained by coralla may reflect environmental factors such as substrate stability and sedimentation rate. The size distribution of coralla on a bed may provide information on population structure and history. As measures of size, we calculate the average linear dimensions of Edgewood colonial coralla (*i.e.*, (maximum width + height) ÷ 2). The common use of basal diameter alone to represent size may bias results because it will inflate values for specimens with low growth forms relative to those with taller forms. Comparisons of size data are made within species; possible differences in growth rates among species would affect size distributions. Sufficient data for comparisons at different localities were obtained from two massive tabulate species (Table 8).

The average and maximum sizes of *Propora thebesensis* are much greater in the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry) than in the Leemon Formation at Section 31 (Thebes North) and the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm) and Section 15 (Calumet) (Table 8). This is especially noteworthy considering that the inferred mean linear growth rate for this species is lower in the *Brevilamnulella* beds than in the other units. The observed size distributions are not likely to have resulted from mechanical sorting; at each of these localities the degree of variability of corallum size is quite large, and very small specimens are present. The attainment of large sizes by corals in the *Brevilamnulella* beds is considered to reflect environmental stability over relatively long periods of time. This is consistent with interpretations of high substrate stability and low sedimentation rate based on the absence of composite coralla, the numerous encrusting relationships, the high proportion of low domical corallum forms, and the low mean growth rate of *P. thebesensis.*

Coralla of *Paleofavosites subelongus* have similar average sizes in the Kissenger Limestone Member of the

Table 8.—Sizes of massive tabulate coralla in selected units within the Edgewood Province. *s.d.* = standard deviation, *c.v.* = coefficient of variation.

species *units* *section-intervals (n = no. of coralla)*	*average linear dimensions* *mean*	*range*	*s.d.*	*c.v.*
Propora thebesensis				
Keel Fm., *Brevilamnulella* beds 23-2 (n = 6)	52.8 mm	16.5–103.0 mm	35.5 mm	67.2
Leemon Fm. 31-1 and 31-1b (n = 10)	34.8 mm	14.5–65.5 mm	18.3 mm	52.6
Bryant Knob Fm. Kissenger Lst. Mbr. 14-1 and 15-1 (n = 14)	30.9 mm	12.5–52.5 mm	12.8 mm	41.4
Paleofavosites subelongus				
Bryant Knob Fm., Kissenger Lst. Mbr. 14-1 and 15-1 (n = 28)	34.4 mm	11.5–67.5 mm	13.8 mm	40.1
Mosalem Fm., coral-rich bedding surface 32-1z (n = 23)	39.5 mm	22.5–56.5 mm	8.8 mm	22.3

Bryant Knob Formation at Section 14 (Higginbotham Farm) and Section 15 (Calumet), and on the coral-rich bedding surface of the Mosalem Formation at Section 32 (Thomson East) (Table 8). At Section 32, however, there is considerably less variability in size, and small coralla with average linear dimensions less than 22.5 mm are absent. This is not likely to have resulted from mechanical sorting; a higher proportion of coralla are in growth orientation and the frequency of abraded specimens is far lower at Section 32 than elsewhere in the Edgewood Province, suggesting comparatively low energy conditions. Perhaps this bedding surface was colonized by an influx of larvae during a very short period of time, and the resulting population was later buried during a single event involving relatively little disturbance of the coralla. Unfortunately, poor preservation of the corallum bases prevents us from determining whether the colonies originated from sexually produced larvae or as a result of asexual fragmentation (see Lee and Noble, 1990).

PALEOENVIRONMENTS

Here we examine the general environments inhabited by Edgewood colonial corals, based on the lithologies in which they occur. Environmental preferences and tolerances are shown to vary among taxa. A diversity gradient is recognized within the Edgewood Province, and is related to an environmental gradient. We are able to make detailed paleoenvironmental determinations, based on comparative taphonomy and paleoecology of colonial corals, for selected stratigraphic units and localities.

A wide spectrum of shallow marine depositional environments is represented by latest Ordovician to earliest Silurian strata in the Edgewood Province (see Text-figs. 2–7). Edgewood colonial corals are typically absent or rare in units considered to represent restricted-marine, low-energy environments. They do not occur in the Wilhelmi Formation at Section 3 (Garden Prairie), where evaporite crystal molds are present in dolomitized mudstone. In general, colonial corals are absent or rare in argillaceous, dolomitized mudstone to wackestone of the Wilhelmi in northeastern Illinois and the Mosalem Formation of northwestern Illinois and eastern Iowa. Exceptions are as follows: the Wilhelmi at Section 37 (Essex), where *Halysites alexandricus, Paleofavosites subelongus,* and *Aulopora* sp. A are present (*H. alexandricus* is common); the coral-rich bedding surface in the Mosalem at Section 32 (Thomson East), where *Propora thebesensis, H. alexandricus,* and *P. subelongus* occur (*P. subelongus* is abundant); and the channel-fill beds in the Mosalem at Section 32, where *Pycnostylus* sp. A is abundant.

Colonial corals are absent or uncommon in other fine-grained or argillaceous units that suggest turbid environments. They have not been found in the "laminated calcilutite unit" of the Keel Formation at Section 24 (Coal Creek), or in shaly beds of the lower Leemon Formation at Section 31 (Thebes North) and the entire Leemon at Section 19 (New Wells). *Paleofavosites subelongus* is rare in dolomitic wackestone of the Cyrene Formation at Section 13 (Bowling Green), and uncommon in argillaceous, dolomitic packstone comprising the unnamed member of the Bryant Knob Formation at Section 18 (Kissenger). Of the Edgewood colonial corals, *P. subelongus* may have been the most tolerant of turbid conditions.

Colonial corals are typically absent or rare in units considered to represent open-marine conditions with the highest energy levels and unstable, shifting substrates. We did not find them in cross-bedded oölites at the base of the Leemon Formation at Section 20

(Short Farm) or in the Noix oölite of west-central Illinois and northeastern Missouri, although *Halysites* has been reported as rare in blocks thought to be from the Noix (Amsden, 1974, fig. 9). Colonial corals are generally absent or rare in oölites of the Keel Formation in south-central Oklahoma. Single specimens of *Halysites alexandricus* were collected at Section 24 (Coal Creek) and Section 25 (Hunton). In the Keel oölite at Section 23 (Lawrence Quarry), however, *Propora thebesensis, Propora savagei, H. alexandricus, Paleofavosites subelongus,* and *Palaeophyllum* sp. are present (*H. alexandricus* is common). A single specimen of *H. alexandricus* is known from a silicified oölite at the top of the Cason Shale at Section 33 (Buffalo River). Of the Edgewood colonial corals, it appears that *H. alexandricus* was most tolerant of very high energy levels and shifting substrates. This is consistent with the conclusion that cateniform growth was advantageous in such environments (Lee and Elias, 1991).

Edgewood colonial corals are typically found in bioclastic packstones to grainstones, some of which are oölitic. These units are considered to represent open-marine, high-energy environments. They contain the most diverse colonial coral associations in the Edgewood Province. Examples are as follows: the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry), where six species were found (*Propora thebesensis, Halysites alexandricus,* and *Catenipora lawrencica* are common); the upper Leemon Formation at Section 31 (Thebes North), where seven species are known (*P. thebesensis* is common); and the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm), where six species occur (*Paleofavosites subelongus* is abundant, *P. thebesensis* is common).

There appears to be a diversity gradient within the Edgewood Province. Eight species of colonial corals representing the Edgewood Assemblage are known from south-central Oklahoma, seven occur in southern Illinois and southeastern Missouri and in northeastern Missouri, and four are present in northeastern Illinois and in northwestern Illinois (Table 1). Western north-central Arkansas is excluded from this analysis because data for that area are based on limited sampling at only one stratigraphic section. The northward decrease in diversity is considered to reflect an environmental gradient from the most open, normal-marine conditions nearest the continental margin in the south, to increasingly restricted conditions farther north into the cratonic interior (see also McAuley and Elias, 1990, p. 27).

Detailed environmental determinations are possible using comparative taphonomy and paleoecology, as discussed above (pp. 22–33). A synthesis of environmental indicators and interpretations for five localities from which sufficient data are available is presented in Table 9. The different lines of evidence provide consistent results at each locality, and permit recognition of subtle as well as major differences in environmental conditions among the stratigraphic units.

The Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm) and Section 15 (Calumet) was deposited in high-energy conditions. Differences in the degree of corallum abrasion suggest that energy levels were slightly lower for the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry), and highest for the upper Leemon Formation at Section 31 (Thebes North). The coral-rich bedding surface in the Mosalem Formation at Section 32 (Thomson East) was deposited in low- to perhaps moderate-energy conditions.

Substrate stability was high during deposition of the Kissenger Limestone in the Bryant Knob Formation and the coral-rich bedding surface in the Mosalem Formation; numerous lines of evidence suggest that it was even higher for the *Brevilamnulella* beds in the Keel Formation. Substrate stability in the Leemon Formation was low. Turbidity was relatively high only in the case of the coral-rich bedding surface. The sedimentation rate was highest for the Leemon and moderate to high for the Kissenger. The *Brevilamnulella* beds and the coral-rich bedding surface were characterized by low sedimentation rates, with numerous lines of evidence suggesting the lowest rate for the *Brevilamnulella* beds.

ASPECTS OF INTRASPECIFIC VARIATION

INTRODUCTION

The quantity of numerical data collected in our study for the definition and description of coral species permits the observation of trends in variation that would not otherwise be recognized. This section begins with a synthesis of certain aspects of variation within species. This provides a basis for the subsequent comparison of patterns of variation among the more common species and orders. General patterns of intracolony, intraspecies, and interspecies variation in Paleozoic colonial corals are, as yet, poorly understood. As described in reviews by Oliver (1968) and Scrutton (1989), many studies have examined aspects of variation within single species or taxonomic groups (*e.g.*, Philip, 1960; Tesakov, 1973; Dixon, 1974; Scrutton and Powell, 1980; Scrutton, 1983, 1990; Bondarenko, 1985; Young and Noble, 1989; Hubmann, 1992). Our study differs from these by examining intracorallum, intralocality, and interlocality variation of all colonial species occurring in a particular stratigraphic interval throughout a large geographic area.

An examination of colonial coral variation must consider several factors. These include ontogeny (development of an individual polyp, as recorded in the corallite), astogeny (development of the colony, as recorded in the corallum), cyclomorphic patterns (periodic morphologic changes recorded by density banding in the corallum), and topomorphic patterns (morphologic differences in different areas of the colony surface, recorded on and in the corallum). Environmental and genetic differences between populations must also be considered. In our analysis we have focused on those structural or design constraints within coralla that resulted in correspondences between numerically analyzed morphologic characters, and on determination of the limits of intraspecific variation within the various groups. Through this methodology, a valid approach to the recognition and definition of colonial coral species may be developed.

VARIATION IN INDIVIDUAL SPECIES

In the following paragraphs, we present an overview of patterns of variation within individual species. The details are documented and illustrated in *Systematic Paleontology.* Variation in numerical characters is described under *Intraspecific variation* for each species. Non-numerical aspects of intraspecific variability are considered under *Description of coralla, Astogeny and corallite increase,* and *Microstructure* for each species.

Propora thebesensis.—Analysis of variation allows us to correlate several morphologic characters. Variation in internal morphology can be related to both geographic locality and growth form.

We have previously analyzed the relationship between size and spacing of tabularia in this species (Young and Elias, 1993). It was demonstrated that an unusually high variability of tabularium diameter within a corallum is commonly related to the density of spacing of tabularia, and is thus partly controlled by structural factors. Many specimens show little variability in tabularium diameter, and have strongly unimodal frequency distributions for this character. Such distributions are similar to those for coralla of many other heliolitid species (Young and Elias, 1993, fig. 2). These strongly unimodal distributions tend to be associated with coralla having more widely spaced tabularia. In coralla with dense tabularium spacing, a larger number of small individuals may have resulted from slower tabularium expansion rates where walls were in contact (Young and Elias, 1993, fig. 5). This yields a broader unimodal or bimodal distribution. The smaller mode of a bimodal distribution probably represents a burst of corallite increase (budding).

As shown above, intracorallum variability of tabularium diameters is related to structural aspects of corallite packing and cyclomorphic patterns. This variability also shows some correlation with locality (see *Intraspecific variation,* pp. 49, 50). Interlocality differences suggest that genetic and/or environmental factors played a role in tabularium size and spacing, and consequently also in the tabularium size-frequency distributions.

There is a strong positive correlation between mean tabularium area and mean corallite area on transverse sections (see *Intraspecific variation,* p. 50). This is similar to the pattern observed in many other heliolitid species (see Young and Noble, 1990a, fig. 3; 1990b, fig. 2).

Variation in these internal characters may be related to corallum growth form. Taller growth forms are most abundant at those localities where tabularia are more densely spaced, such as Section-intervals 31-1 and 31-1b (Thebes North), and Section-interval 14-1 (Higginbotham Farm). Lower forms are most common where tabularia are broadly spaced, as in Section-interval 23-2 (Lawrence Quarry). Taller growth forms also tend to be associated with wider vertical spacing of tabulae and dissepiments (see *Growth Rate,* p. 31). The presence of such relationships may indicate that internal morphology was more strongly tied to environment than is commonly accepted, but it also suggests that growth forms in a single species could have varied due to genotypic differences between populations.

Tabulations of morphologic characters at the major localities (Tables 10, 11) illustrate the close similarities between specimens from most places, but also show that coralla from Section-interval 23-2 tend to lie at one end of the spectrum of variation. The lower growth forms, widely spaced crenulate tabularia, thick walls, well developed septa, and more closely spaced horizontal elements that are typical of this locality may have developed as a response to the distinct environmental conditions prevalent there (see *Growth Form,* pp. 29, 30; *Paleoenvironments,* p. 34). It is also possible, however, that the geographic distance between Section 23 (Lawrence Quarry) and the other major localities may have permitted a degree of reproductive isolation, resulting in significant genotypic differences.

Propora savagei.—Aspects of intraspecific variation analyzed here show patterns typical of the Proporidae. These include the unimodal frequency distribution for tabularium diameter within a corallum and the positive correlation between tabularium area and corallite area (see *Intraspecific variation,* p. 57). The frequency distribution has a slight negative skewness. This was probably caused by a low rate of corallite increase.

Significant variation between localities is observed

Table 9.—Environmental interpretations for selected units within the Edgewood Province, based on lithologies and characteristics of colonial corals including *Propora thebesensis* and *Paleofavosites subelongus*. × indicates an environmental interpretation (for explanations, see *The Edgewood Colonial Corals*, pp. 22–34).

	energy level					*substrate stability*			*turbidity*	*sedimentation rate*					
units *section-intervals* *environmental indicators*	*highest*	*high*	*moderately high*	*moderate*	*low*	*highest*	*high*	*low*	*relatively high*	*highest*	*high*	*moderately high*	*moderate*	*low*	*lowest*
Keel Fm., *Brevilamnulella* beds															
23-2															
lithology: oölitic, bioclastic packstone–grainstone; aligned shells	—	×	—	—	—	—	×	—	—	—	—	—	—	—	—
proportion abraded (massive tabulate coralla): high	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
degree of abrasion (massive tabulate coralla): moderately high	—	—	×	—	—	—	—	—	—	—	—	—	—	—	—
proportion overturned (massive tabulate coralla): high	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
proportion noncomposite (tabulate coralla): high	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—
proportion of colonial coralla with encrusters: highest	—	—	—	—	—	×	—	—	—	—	—	—	—	—	×
proportion of colonial coralla that are encrusters: highest	—	—	—	—	—	×	—	—	—	—	—	—	—	—	×
proportion of domical growth forms (*P. thebesensis*): highest	—	—	—	—	—	×	—	—	—	—	—	—	—	—	×
proportion of domical forms with flat bases (*P. thebesensis*): highest	—	—	—	—	—	×	—	—	—	—	—	—	—	—	×
proportion of low growth forms (*P. thebesensis*): highest	—	—	—	—	—	×	—	—	—	—	—	—	—	—	×
inferred mean growth rate (*P. thebesensis*): lowest	—	—	—	—	—	×	—	—	—	—	—	—	—	—	×
average and maximum corallum size (*P. thebesensis*): highest	—	—	—	—	—	×	—	—	—	—	—	—	—	—	×
Leemon Fm.															
31-1 and 31-1b															
lithology: skeletal grainstone; moderately well-rounded grains	—	×	—	—	—	—	—	×	—	—	—	—	—	—	—
proportion abraded (massive tabulate coralla): high	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
degree of abrasion (massive tabulate coralla): highest	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—
proportion noncomposite (tabulate coralla): lowest	—	—	—	—	—	—	—	×	—	—	—	—	—	—	—
proportion of colonial coralla with encrusters: low	—	—	—	—	—	—	—	×	—	—	×	—	—	—	—
proportion of colonial coralla that are encrusters: none	—	—	—	—	—	—	—	×	—	—	×	—	—	—	—
proportion of domical growth forms (*P. thebesensis*): lowest	—	—	—	—	—	—	—	×	—	×	—	—	—	—	—
proportion of columnar growth forms (*P. thebesensis*): highest	—	—	—	—	—	—	—	×	—	×	—	—	—	—	—
inferred mean growth rate (*P. thebesensis* and *P. subelongus*): high	—	—	—	—	—	—	—	×	—	—	×	—	—	—	—
Bryant Knob Fm., Kissenger Lst. Mbr.															
14-1 and 14-2															
lithology: fossiliferous grainstone; aligned clasts	—	×	—	—	—	—	×	—	—	—	—	—	—	—	—
proportion abraded (massive tabulate coralla): high	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
degree of abrasion (massive tabulate coralla): high	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—

Table 9.—Continued.

units *section-intervals* *environmental indicators*	*energy level*					*substrate stability*			*turbidity*	*sedimentation rate*					
	highest	*high*	*moderately high*	*moderate*	*low*	*highest*	*high*	*low*	*relatively high*	*highest*	*high*	*moderately high*	*moderate*	*low*	*lowest*
proportion overturned (massive tabulate coralla): high	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
proportion noncomposite (tabulate coralla): high	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—
proportion of colonial coralla with encrusters: moderately low	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—
proportion of colonial coralla that are encrusters: none	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
proportion of domical growth forms (*P. thebesensis* and *P. subelongus*): moderate	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—
proportion of columnar growth forms (*P. thebesensis*): moderate	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—
inferred mean growth rate (*P. thebesensis* and *P. subelongus*): moderate	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—
15-1															
lithology: grainstone	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
proportion abraded (massive tabulate coralla): high	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
degree of abrasion (massive tabulate coralla): high	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
proportion noncomposite (tabulate coralla): high	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—
proportion of colonial coralla with encrusters: moderately low	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—
proportion of colonial coralla that are encrusters: none	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
proportion of domical growth forms (*P. thebesensis* and *P. subelongus*): low	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
proportion of high growth forms (*P. thebesensis*): highest	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—
inferred mean growth rate (*P. thebesensis* and *P. subelongus*): moderate	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—
Mosalem Fm., coral-rich bedding surface															
32-1z															
lithology: mudstone–wackestone	—	—	—	—	×	—	×	—	×	—	—	—	—	—	—
proportion abraded (massive tabulate coralla): low	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—
degree of abrasion (massive tabulate coralla): low	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—
proportion overturned (massive tabulate coralla): moderate	—	—	—	×	—	—	—	—	—	—	—	—	—	—	—
proportion noncomposite (tabulate coralla): high	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—
proportion of colonial coralla with encrusters: low	—	—	—	—	—	—	—	—	×	—	—	—	—	—	—
proportion of colonial coralla that are encrusters: none	—	—	—	—	—	—	—	—	×	—	—	—	—	—	—
proportion of domical growth forms (*P. subelongus*): highest	—	—	—	—	—	×	—	—	—	—	—	—	—	—	×
proportion of domical forms with flat bases (*P. subelongus*): low	—	—	—	—	—	—	×	—	—	—	—	—	—	×	—

Table 10.—Interlocality variation in qualitatively defined morphologic characters of *Propora thebesensis* in the east-central United States. P = predominant, C = common, R = rare or weakly developed, A = absent.

	sections/section-intervals						
characters	*23-2*	*31-1 and 31-1b*	*14-1*	*15-1*	*16*	*18*	*32-1c*
columnar forms	A	P	C	A	—	—	—
high bulbous and domical forms	C	C	C	P	—	—	—
low bulbous and domical forms	C	C	R	A	—	—	—
smooth-walled tabularia	R	P	P	C	R	—	C
crenulate tabularia	P	R	C	C	P	—	R
subpolygonal tabularia	R	C	C	C	C	P	R
cyclomorphic thickening	C	R	R	R	—	—	—

in comparisons of coralla from Section 20 (Short Farm) with those from the other localities. These differences may have evolutionary significance, and are considered in detail elsewhere (see *Discussion,* p. 58).

Propora speciosa.—Coralla are very consistent in numerically analyzed characters, but differ visibly in patterns of thickening of skeletal elements. These patterns are not correlated with interlocality variability; some of the greatest differences occur between specimens from the same locality (see *e.g.,* Pl. 7, figs. 1, 7). The corallum from the upper Mosalem Formation at Section 32 (Thomson East) (see Pl. 7, fig. 8) is younger than and is separated by a considerable geographic distance from the specimens from Section 31 (Thebes North) and the Gale Section. Nevertheless, it is similar to them and its numerical characters are mostly close to the species means (see *Description of coralla,* p. 59; *Discussion,* p. 61).

A relatively low degree of variability is observed in specimens of *Propora speciosa* from the east-central United States. This is consistent with the character of this species as noted by Dixon (1974, pp. 581, 582) in his discussion of material from the Ellis Bay Formation on Anticosti Island, Québec, and also as commented on by Scrutton (1989, p. 40) (see also *Comparisons of Species,* p. 42).

Halysites alexandricus.—Although this species is common in the study region, variation between localities is not distinct. This observation may be related to preservational problems, since the fragmentary nature of much material limits numerical analysis.

Paleofavosites subelongus.—This species shows a high degree of variability in several important morphologic characters. It is like other favositids (see Scrutton, 1989, pp. 40, 41; Lee and Noble, 1988, p. 38) in often exhibiting extreme variation in intracorallum corallite size. Mean corallite sizes can also be quite different between coralla. Since this parameter is commonly used to discriminate species, we document this variability and examine possible controls of corallite size. Other characters of *Paleofavosites subelongus* that show interesting types of variation include growth form, initial corallum astogeny, and the degree of development or thickening of skeletal characters.

Corallite size-frequency distributions of *Paleofavosites subelongus* can be quite different from one transverse section to another, both within and between coralla. For this reason, we used this species as an example in an examination of the relationship between favositid corallite size and polygonality (number of sides) (see Young and Elias, 1993). Differences in the variability of corallite dimensions between transverse sections from a single corallum are apparently related to rate and periodicity of corallite increase (Young and Elias, 1993, p. 288; see also Scrutton and Powell, 1980, p.

Table 11.—Interlocality variation in quantitatively defined morphologic characters of *Propora thebesensis* in the east-central United States. "A" and "B" refer to frequency of data points above and below arbitrary lines in Text-figure 14B, D, F.

	section-intervals			
characters	*23-2*	*31-1 and 31-1b*	*14-1*	*15-1*
tabularium area : corallite area				
A (tabularia closely spaced)	1 (7%)	8 (67%)	11 (79%)	4 (40%)
B (tabularia farther apart)	13 (93%)	4 (33%)	3 (21%)	6 (60%)
spacing of tabulae and dissepiments				
A (elements close together)	7 (100%)	1 (17%)	1 (9%)	—
B (elements farther apart)	0 (0%)	5 (83%)	10 (91%)	—
wall thickness and septal development				
A (walls thick, septa longer)	9 (69%)	1 (10%)	3 (33%)	1 (20%)
B (walls thin, septa short or absent)	4 (31%)	9 (90%)	6 (67%)	4 (80%)

480). New corallites expanded slowly due to the physical constraints caused by corallite packing (Young and Elias, 1993, pp. 289, 290, table 1). The size-frequency distribution of corallites having six and more sides on any given transverse section of *P. subelongus* is virtually normal. This supports the recognition of such corallites as mature individuals (see Young and Elias, 1993, pp. 284, 286, fig. 3).

Corallite size is correlated with the degree of development and thickening of several skeletal characters, including wall thickness, relative septal length, and the diameter of corner pores (see *Intraspecific variation,* p. 85). The relationship between average corallite dimension and pore diameter is comparable to that described by Tesakov (1973, figs. 8, 9) for *Favosites* Lamarck and *Calamopora* Goldfuss (*Paleofavosites*) from the Silurian of Siberia. However, a relationship between corallite size and the development of pores, wall thickness, and septal length has not, to our knowledge, been previously documented. Such a relationship certainly has not been observed in any of the other tabulates included in the present study. The correlation among these characters supports the idea that growth of favositid corallites was largely controlled by structural constraints imposed by colony design; these constraints apparently extended beyond the physical corallite packing discussed by Young and Elias (1993).

Variation in mean corallite size is correlated with general differences in colony growth form between localities. Coralla having domical growth forms and flat bases tend to have larger corallites than do those having bulbous or columnar forms and conical bases. This difference may be related to the primary growth habit of each corallum; an initially broad divergence of corallites provided more space for corallites to expand to large sizes within the corallum. The relationship between average corallite dimension and colony form is complex because form could change during astogeny, and factors such as colony reorientation and partial mortality could have affected the final form.

The shape of the corallum base itself seems to have resulted more from a response to local conditions than from deterministic growth, although the initial pattern indicates a degree of genetic control. Serial sections through the absolute base of a corallum show that the protocorallite (formed by the polyp that founded the colony) was joined initially by four hysterocorallites (formed by polyps that arose through budding). This pattern is very similar to that described by Girty (1895) for four species of *Favosites,* except that the location of the hysterocorallites in Girty's specimens was generally more regular than is the case for the corallum of *Paleofavosites subelongus.* Subsequent growth of the base, however, shows no indication of dominance on the part of the protocorallite or the initial hysterocorallites, and the continued growth of any corallite seems to have been related to its position in the corallum rather than to "seniority." The shapes of bases of individual coralla are consistent with local environmental conditions inferred from other indicators, such as lithology and abrasion of coralla (see *Growth Form,* p. 29).

Table 12.—Interlocality variation in qualitatively defined morphologic characters of *Paleofavosites subelongus* in the east-central United States. P = predominant, C = common, R = rare or weakly developed, A = absent.

	sections/section-intervals						
characters	*31-1*	*14-1*	*15-1*	*18*	*S of Clarks-ville*	*near Edge-wood*	*32-1z*
columnar forms	—	C	A	—	—	—	R
high bulbous forms	—	C	C	—	—	—	R
low bulbous forms	—	C	C	—	—	—	R
high domical forms	—	C	A	—	—	—	C
low domical forms	—	C	C	—	—	—	C
long septa	A	C	R	P	C	P	C
mid-wall pores	A	R	A	A	A	R	R
widely spaced tabulae	P	C	C	C	P	C	P
closely spaced tabulae	R	C	C	C	R	C	R
cyclomorphic thickening	A	C	C	R	C	R	R

Tabulations of morphologic characters (Tables 12, 13) indicate that similar morphotypes occur at several localities, and that much of the interlocality variation is not systematic. It is difficult to make general comparisons between the distribution of growth form and that of most other characters because form data for most localities are not available; correspondences between form and average corallite dimension are discussed above. Coralla from Section-interval 31-1 (Thebes North) lie at one end of the spectrum of variation in internal morphology, characteristically having small corallites, short septa, widely spaced tabulae, and little or no cyclomorphic thickening. Specimens from 5 km south of Clarksville, Missouri, also have small corallites and widely spaced tabulae, but some of these have longer septa and a higher degree of cyclomorphic thickening. Coralla from Section-interval 14-1 (Higginbotham Farm) and Section-interval 15-1 (Calumet) are highly variable, including most of the range of variation of this species, whereas those from Section-interval 18-1 (Kissenger) and from the Cyrene Formation near Edgewood, Missouri, generally have long septa, variable spacing of tabulae, and rare cyclomorphic thickening. The suite of coralla from Section-interval 32-1z (Thomson East) is distinctive; these possess large, thin-walled corallites with widely spaced tabulae.

The occurrence of mid-wall pores in this species may have stratigraphic and evolutionary significance. Mid-

Table 13.—Interlocality variation in quantitatively defined morphologic characters of *Paleofavosites subelongus* in the east-central United States. "A" and "B" refer to frequency of data points above and below arbitrary lines in Text-figures 25A, B, 26A; c.v. = coefficient of variation.

	sections/section-intervals				
characters	*31-1*	*14-1*	*15-1*	*S of Clarksville*	*32-1z*
average corallite dimension					
A (larger corallites)	0 (0%)	19 (50%)	2 (29%)	0 (0%)	24 (73%)
B (smaller corallites)	6 (100%)	19 (50%)	5 (71%)	5 (100%)	9 (27%)
c.v. of avg. corallite dimension and c.v. of polygonality					
A (more variable size and polygonality)	4 (67%)	23 (61%)	5.5 (79%)	1 (20%)	16 (48%)
B (less variable size and polygonality)	2 (33%)	15 (39%)	1.5 (21%)	4 (80%)	17 (52%)
wall thickness and average corallite dimension, 6+ sides					
A (walls relatively thick)	—	18 (58%)	3 (43%)	—	2 (33%)
B (walls relatively thin)	—	13 (42%)	4 (57%)	—	4 (67%)

wall pores are absent in coralla from all stratigraphic intervals considered to be latest Ordovician (Gamachian), such as Section-intervals 23-2 and 23-3 (Lawrence Quarry), and Section-interval 31-1. They are, however, found in small numbers in some intervals where rocks are possibly earliest Silurian (early Rhuddanian?; *e.g.,* Section-interval 14-1) or definitely earliest Silurian (early Rhuddanian; *e.g.,* Section-interval 32-1z). This pattern, along with the greater abundance of mid-wall pores in the slightly younger (late Rhuddanian), apparently descendant species *Paleofavosites* sp. cf. *P. subelongus* from Section-interval 32-1c (Thomson East), suggests that this character appeared within the species lineage.

Paleofavosites adaensis.—This species exhibits little intercorallum variation in most morphologic characters, but there are distinct differences between localities for corallite size distributions and spacing of tabulae. These characters show a correlation with colony growth form (see *Intraspecific variation,* p. 93). At those localities where forms are bulbous or domical, corallite size distributions are somewhat variable and tabulae are widely spaced. Where coralla have tabular forms, corallite size distributions are regular and tabulae are more closely spaced.

Aulopora sp. A.—This species occurs at two localities. Variation in corallite size distribution for the two specimens from Section-interval 23-2 (Lawrence Quarry) shows an unusual pattern. Visual observation of both specimens suggests that each includes several small coralla comprising one or a few corallites; corallites expanded rapidly above their bases and are rarely observed to be connected with one another (Pl. 20, fig. 1). This suggestion is also supported by the frequency distribution of corallite and tabularium sizes in one specimen, which is dominated by small corallites (see *Intraspecific variation,* p. 98). In contrast with this, the size-frequency curve for a single, larger auloporid corallum from the Devonian of southwest England (Scrutton, 1990, fig. 11a) is approximately normal, and is similar to the curves commonly seen for massive coenenchymal Tabulata.

COMPARISONS OF SPECIES

Comparisons of the patterns of variation in different species indicate that inherent variabilities of different coral orders are not the same, and that certain types of variation tend to recur among species and among orders. Some of the general similarities and differences among taxa are linked principally to the structural factors that controlled the ways in which colonial corals were able to grow. Genotypic and ecophenotypic factors acted in concert with the structural control of growth to determine variation within the individual species.

Degrees of variability.—From the discussions under *Variation in Individual Species,* above, it is apparent that some colonial coral species are much more variable than are others. The possible causes of such differences in variability must be considered, because the limits of variability must be known in order to properly define species within each order. Species belonging to some orders have more variable corallite sizes due to inherent design constraints. Differences in variability are also significant because they may reflect disparity in the morphologic plasticity of species, which may explain why some species were able to live in a greater variety of environments than were others.

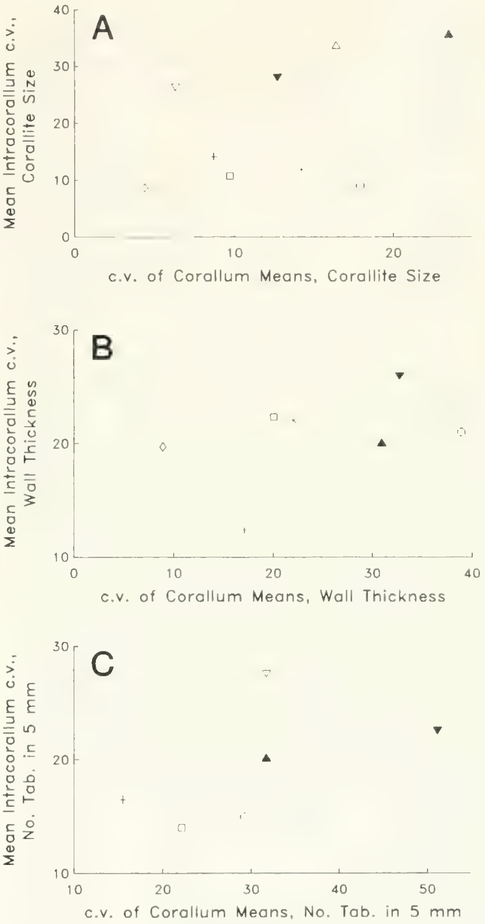
Differences in variability of fossil invertebrate taxa are quite commonly discussed in the literature, but numerical comparisons of the amount of variation are relatively rare. For a numerical description of intracorallum and intercorallum variability for each parameter, we follow Oliver (1968, pp. 27, 28), Scrutton (1989, pp. 39, 40), and Stearn (1989, pp. 45, 46) in using the coefficient of variation (c.v.) (Simpson *et al.,* 1960). The c.v. can be readily used to compare different types of numerical data because it is dimensionless. It is generated using the following formula:

$$\text{c.v.} = \frac{\text{standard deviation}}{\text{mean}} \times 100.$$

Graphs of mean intracorallum c.v. *versus* the c.v. of corallum means are plotted for three parameters: corallite size, wall thickness, and spacing of tabulae (Text-fig. 11). Intracorallum variability of corallite size for each species of *Paleofavosites* (Order Favositida) is two to three times as great as for any species of *Propora* (Order Heliolitida), or *Halysites* and *Catenipora* Lamarck (Order Halysitida) (Text-fig. 11A). A similar pattern was noted by Scrutton (1989, p. 40, fig. 4b) in a comparison of favositids and heliolitids. The basis for high intracorallum variability in corallite size of favositids is in their design. Lateral expansion of favositid offsets was slow, with rates governed by the lateral expansion of the growth surface and the degree of contraction of surrounding corallites; for this reason transverse sections frequently include substantial numbers of immature individuals (see Young and Elias, 1993, pp. 283, 288, fig. 2). The coenosteal and cateniform growth habits of heliolitids and halysitids permitted new corallites to expand much more rapidly. Most of the species of *Paleofavosites* included in the present study have intraspecific variabilities for mean corallum corallite size similar to those of the other tabulates. The one exception is *Paleofavosites subelongus;* the greater intraspecific variability of size in that species may be related to its ability to grow in a broad variety of environments (see *Paleoenvironments,* pp. 33, 34).

Although intracorallum and intraspecific variation in wall thickness can be substantial (Text-fig. 11B), there are no obvious differences among orders. Variation in wall thickness is not related in any recognizable way to the structural design of most of these taxa; the lack of such a connection probably accounts for the absence of distinctions for this character.

The graph for spacing of tabulae indicates that both intracorallum and intraspecific variability are greater for species of *Paleofavosites* than for other taxa (Text-fig. 11C). This greater variability appears to be related to two factors: cyclomorphic growth and interlocality variation. In general, the species of *Paleofavosites* occurring in the study region show a greater amount of cyclomorphic variation in spacing of tabulae than do the other colonial corals. Cyclomorphic growth patterns are particularly marked in *Paleofavosites* sp. A (Pl. 19, fig. 12), explaining the large mean intracoral-



Text-figure 11.—Comparison of coefficients of variation (c.v.) for selected parameters in several species of Tabulata from the east-central United States. **A**, Mean intracorallum c.v. *versus* intraspecific c.v. of corallum means for corallite size (tabularium diameter of heliolitids, tabularium dimension (length) of halysitids, average corallite dimension of favositids). **B**, Mean intracorallum c.v. *versus* intraspecific c.v. of corallum means for wall thickness. **C**, Mean intracorallum c.v. *versus* intraspecific c.v. of corallum means for number of tabulae in unit 5 mm. Graphs are based on data included in Tables 15, 18, 19; species included in graphs all had four or more coralla measured for the given parameter. Symbols for species: □ *Propora thebesensis;* ○ *Propora savagei;* ◇ *Propora speciosa;* + *Halysites alexandricus;* × *Catenipora lawrencica;* ▲ *Paleofavosites subelongus;* △ *Paleofavosites* sp. cf. *P. subelongus;* ▼ *Paleofavosites adaensis;* ▽ *Paleofavosites* sp. A.

lum c.v. for that species. In *Paleofavosites adaensis,* different tabular spacings are associated with the variation in corallum growth form seen at different localities; this is responsible for the great variability of corallum means for the species.

Among the non-favositid corals, *Propora savagei* and *Propora speciosa* are remarkable for representing the extremes of intraspecific variability in corallite size and wall thickness. The remarkable consistency among specimens of *P. speciosa* has already been commented upon (see *Propora speciosa,* p. 38). The high degree of intraspecific variability in *P. savagei* reflects the differences between coralla from Section 20 (Short Farm) and those from other localities (see *Discussion,* p. 58).

Shared patterns of variability.—Species of massive Tabulata having coenenchymal and cerioid growth habits both show connections between external corallum growth form and aspects of internal morphology that are related to corallite size and packing. In *Propora thebesensis,* coralla having densely spaced tabularia tend to exhibit a greater variability of tabularium diameter than do those having more broadly spaced tabularia. Tabularia are often more densely spaced at localities where taller growth forms predominate, and more broadly spaced where lower growth forms are common. The pattern for *Paleofavosites adaensis* is analogous; corallite size distributions are more variable at localities where forms are bulbous or domical than at localities where tabular forms predominate. The situation for *Paleofavosites subelongus* is slightly different; the internal parameter related to growth form is average corallite dimension (corallite size). Coralla of *P. subelongus* having domical growth forms and flat bases tend to have larger corallites than do those having bulbous or columnar forms and conical bases.

In each of these cases, control on tabularium and corallite size was probably exerted by the internal space constraints determined by external corallum form. Where external forms restricted lateral expansion of the individual modules, tabularia or corallites became smaller and/or expanded more slowly (producing more variable size distributions). The influence of environmental factors on corallum growth form was apparently similar in *Propora thebesensis* and *Paleofavosites subelongus* (see p. 28), and variation in internal characters of these species may have been partly under environmental control.

SYSTEMATIC PALEONTOLOGY

INTRODUCTION

Analysis of variation is integral to the species concept for Paleozoic colonial corals. The general approach that we use is similar to that outlined by Scrutton (1989, pp. 40, 41). Valid species can be recognized only when intraspecific variation based on a number of coralla is thoroughly documented. A very high degree of intraspecific variability can be accepted, but variation in important numerical and non-numerical characters must be reasonably continuous. Species are separated from one another by morphologic gaps (*e.g.,* see Young and Noble, 1990b, fig. 2). In this study we include separate descriptions of intraspecific variation under those species for which sufficient data are available; an overview and synthesis that compares variation in the different species and orders is presented above (see *Aspects of Intraspecific Variation,* pp. 34–42). All aspects of morphology that can be described, including astogeny, corallite increase, microstructure, and growth form, are considered when defining species. In general, the most useful characters for species discrimination are the form of basic structural elements such as walls, septa, and tabulae, and certain measured parameters including tabularium or corallite diameter and corallite area (see *Biometric Methods,* pp. 43, 44).

In many respects, the systematic difficulties involved in the discrimination of Paleozoic colonial coral species are comparable to the problems faced by workers examining living corals of the subclass Scleractinia Bourne (*e.g.,* Coates, 1984). Some species of modern corals show little variability, but others are extremely variable (Best *et al.,* 1984). Analysis of large numbers of scleractinian colonies is essential for determining patterns of intracolony and intraspecies variability (*e.g.,* see Veron and Pichon, 1976; Foster, 1985).

Our suprageneric classification is similar to that given in Hill (1981), with two significant exceptions. First, we consider the Halysitida to be a separate order, rather than a suborder of the Heliolitida. Second, the subfamily Paleofavositinae Sokolov is included as a junior synonym of the Favositinae Dana. Explanations of these differences in approach are provided in the discussions under those groups, below. Suprageneric taxa and genera are discussed if our work has increased the knowledge and understanding of the group.

Many of the morphologic terms that we use to describe both tabulate and rugose corals follow Hill (1981, pp. F6–F36, F430–F456). Some terms for heliolitid morphology are taken from Dixon (1974). Categories for corallum growth form are described in *Growth Form* (pp. 27, 28). General terms for corallite increase are from Oliver (1968, pp. 19–21) and (Hill, 1981, pp. F437, F438); descriptors of increase in halysitids are after Webby and Semeniuk (1969, pp. 353–356) and Webby (1975). Detailed terms are not used to distinguish astogenetic stages because this would impose an arbitrary structure on phenomena that are poorly understood.

A total of 361 specimens from the east-central United States are identified herein; these are assigned to 21 species. Both transverse and longitudinal thin sections were made of all collected coralla; specimens were identified and measured if possible. Species descriptions and diagnoses are based on all identified material. A group of thoroughly documented, conspecific coralla is assigned to a previously described species if a definite identification can be made, using comparison with type material. A new species is named if sufficient material is available so that we can accurately assess morphology and variability, and can not assign that material to a previously described species. In some cases, a group of coralla clearly belongs to a single species, but can not be completely described due to insufficient numbers or poor preservation. If it has obvious affinities with or is comparable to a known species, it is named with "sp. aff." or "sp. cf.," respectively. Such a group of conspecific coralla is assigned a letter designation ("sp. A") if it is not sufficiently similar to a known species. The designation "sp." is used for a group of coralla belonging to *Palaeophyllum* because we are not certain that all included coralla are conspecific.

Each synonymy includes those taxa we consider to be synonymous, along with possible synonyms and others that are very similar. A similar taxon that is not definitely synonymous with the described group is given the appropriate designation, as follows: [*aff.*] if it has definite affinities, [*cf.*] if it is comparable, and [?] if it is a questionable synonym.

BIOMETRIC METHODS

Many Paleozoic colonial corals are morphologically simple, possessing several characters that are easily quantified. Such characters are good indicators of variation, but they should be assessed carefully, and must not be used to the exclusion of qualitatively defined features for species discrimination. Many of the measurements applied here are the same as or similar to parameters used in the following studies: Dixon (1974, pp. 568–570) and Young and Noble (1990a, pp. 44, 45) for Heliolitida; Young *et al.* (1991, pp. 715, 716) for Halysitida; and Sutton (1966, p. 257) and Young and Elias (1993) for Favositida. Measurements are made on the mature part of each corallum, if it can be recognized. For linear measurements, a sample of 20 corallites per corallum is considered to give a reasonable representation of that specimen (Oliver, 1968, p. 27; Dixon, 1974, p. 568; Scrutton, 1989, p. 40). Where possible, at least 20 corallites are measured within a contiguous area on each thin section for each appropriate parameter. An exception is made for average corallite dimension and polygonality of favositids, where all corallites in a contiguous area are measured until data are obtained on at least 20 corallites having six and more sides (such corallites are considered to be adults; see Young and Elias, 1993). Biometric methods pertaining to growth form are described in *Growth Form* (pp. 27, 28).

The following parameters are measured or counted on transverse sections:

Tabularium diameter (TaD).—For heliolitids, the order Auloporida Sokolov, and tetradiids, this character is measured internally from wall to wall where walls are least thickened by septal development.

Tabularium dimensions (TaD (L), TaD (W)).—Length (L, along the rank) and width (W, across the rank) of halysitid tabularia are measured separately because most halysitid corallites are ovate or elliptical in transverse section. Measurement is done internally from wall to wall.

Tabularium area (TaA).—For heliolitids, tabularium area is calculated from the diameter. For halysitids, it is calculated as the area of an ellipse based on the tabularium dimensions (length and width).

Average corallite dimension (ACD (all), ACD (6+)).—This parameter, measured in favositids, is similar to the average transverse axis measurement of Sutton (1966, p. 257). Two measurements of dimension for each corallite are made at right angles to one another, between corallite midwalls. The mean of these is used to describe corallite size. For a corallite that is not equidimensional, the axis around which the corallite is closest to being bilaterally symmetrical is used to orient the first measured dimension. Data are presented separately for all measured corallites and for those having six and more sides.

Corallite diameter (CoD).—The external corallite diameter is measured for auloporids, tetradiids, and rugosans.

Corallite area (CoA).—This parameter is quantified for heliolitids and favositids. A unit area of 1 cm^2 is placed on the part of the transverse section on which measurements of tabularium diameter or average corallite dimension are made; all corallites within that area are counted. Half and quarter corallites are included in the count. The mean corallite area, in mm^2, is calculated from the inverse of this count.

Tabularium area : corallite area (TaA:CoA).—The ratio between tabularium area and corallite area of heliolitids is quantified as a measure of density of tabularium spacing.

Polygonality (Pol).—For favositids, polygonality (the number of sides per corallite) is determined as the number of other corallites a particular corallite is in contact with.

Tubule diameter (TuD).—For heliolitids having tubular coenenchymes, internal diameter of each tubule is measured.

Tubule dimensions (TuD (L), TuD (W)).—For halysitids having tubules between their corallites, internal tubule dimensions are separated into length (L, along the rank) and width (W, across the rank).

Wall thickness (WT).—This character is measured for all corals. In heliolitids, thickness of the tabularium wall is measured between septa, where it is least affected by trabecular thickening. In halysitids, wall thickness is measured at the midpoint of the side of each corallite. In favositids, the thickness of each shared corallite wall is measured between septa, where it is less affected by thickening. In auloporids and tetradiids, the corallite wall is measured between septa, where it is least affected by thickening. For rugosans, this character is measured at the midpoint between a pair of septa.

Pore diameter (PoD).—The diameter of corner pores is measured in favositids.

Length of septa (LS).—For heliolitids, halysitids, and auloporids, the length of septa in each corallite is determined as a percentage of the tabularium radius. In favositids and tetradiids, the percentage of the corallite radius is used. For rugosans, the length of major septa is determined as a percentage of the corallite radius.

Number of major septa (NS).—The number of major septa in each rugosan corallite is counted.

The following parameters are measured or counted on longitudinal sections:

Number of tabulae in 5 mm (Ta5).—For all groups, the number of corallite tabulae in 5 mm is counted along the axis of each corallite. One end of the unit 5 mm is placed directly over one tabula, which is not included in the count.

Number of septa in 5 mm (Se5).—For favositids, the number of septal spines in 5 mm is counted along the wall of each corallite. One end of the unit 5 mm is placed directly over one septum, which is not included in the count.

Number of dissepiments in 5 mm (Di5).—The number of heliolitid coenenchymal dissepiments in 5 mm is measured along a vertical transect at the midpoint between two tabularia. One end of the unit 5 mm is placed directly over one dissepiment, which is not included in the count.

Number of tabulae in 5 mm : number of dissepiments in 5 mm (Ta5:Di5).—The ratio between vertical densities of tabulae and dissepiments in heliolitids is calculated as a measure of the relative spacing of these horizontal elements.

Thickness of cycles (TC).—The thickness of cycles is measured in coralla exhibiting obvious cyclomorphic variation in density of spacing and thickening of skeletal elements. A cycle is defined as one pair of dense and less dense growth bands.

COLLECTORS AND REPOSITORIES

Specimens examined during this study are identified by a repository abbreviation and catalogue number. Unless stated otherwise, they were collected by R. J. Elias, G. A. Young, and V. L. F. Young in 1990. Abbreviations of repositories are listed below.

GSC:	Geological Survey of Canada, Ottawa, Ontario, Canada.
ROM:	Royal Ontario Museum, Toronto, Ontario, Canada.
UI:	University of Illinois at Urbana–Champaign, Urbana, Illinois, U.S.A.
USNM:	National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.
YPM:	Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A.

SYSTEMATICS

Class **ANTHOZOA** Ehrenberg, 1834

Subclass **TABULATA** Milne-Edwards and Haime, 1850

Order **HELIOLITIDA** Frech, 1897

Diagnosis.—Tabulata having massive coralla of variable growth form. Tabularia separated by coenenchyme. Septa number 12, each consisting of a trabecular or laminar base that may possess a row of distinct spines; may be absent. Tabulae commonly complete. Increase coenenchymal.

Remarks.—Our concept of the Heliolitida is essentially the same as that outlined by Hill (1981, p. F602) for the Heliolitina Frech. Hill (1981, pp. F602, F603) included the Halysitina Sokolov in the Heliolitida. We consider the Halysitida to be a separate order (see *Discussion* under Order Halysitida, pp. 66, 67).

Family **PROPORIDAE** Sokolov, 1949

Genus **PROPORA** Milne-Edwards and Haime, 1849

Propora Milne-Edwards and Haime, 1849, p. 262.
Lyellia Milne-Edwards and Haime, 1851, pp. 150, 226.
Pinacopora Nicholson and Etheridge, 1878, p. 52.
Calvinia Savage, 1913, pp. 65, 66 [*non* Nutting, 1900].
Cavella Stechow, 1922, p. 152.
Koreanopora Ozaki, 1934, p. 68.
[?] *Acdalopora* Bondarenko, 1958, p. 215.
[?] *Mcleodea* Flower and Duncan, 1975, pp. 186, 187.

Type species.—By monotypy: *Porites tubulata* Lonsdale (1839, p. 687, pl. 16, figs. 3, 3a–f); Woolhope

Limestone (upper Lower Silurian, Wenlock), Welsh Borderland, U.K.

Diagnosis.—Proporidae with tabularia of smooth or crenulate outline, separated from one another by coenenchyme composed of dissepimentate plates. Twelve septa have basal ridges that may bear spinose adaxial extensions; septal bases commonly exhibit trabecular thickening which may extend outward into coenenchyme. Other trabeculae may occur between septa in corallite walls, or in coenenchyme. Corallite walls composed of vertically oriented trabeculae, or with lamellar appearance where trabeculae are not developed; complete or incomplete. Tabulae usually complete.

Discussion.—Our concept of *Propora* is similar to those recently outlined by Dixon (1974, p. 570), Laub (1979, pp. 331, 332), Hill (1981, p. F612), Scrutton (1985, p. 35), and Young and Noble (1990b, pp. 187, 188). The present examination of species from the east-central United States, however, demonstrates that members of this genus can have a wide variety of wall structures.

Calvinia (= *Cavella*) is synonymized with *Propora*, following re-examination of the type material. Savage's (1913) recognition of *Calvinia* as a distinct genus was based on the incorrect interpretation of vertically oriented coenenchymal trabeculae as tubules. The type specimen of *Calvinia edgewoodensis* (UI X-850), from the Leemon Formation (uppermost Ordovician, Gamachian) at the Gale Section is conspecific with *Propora speciosa* (see *Discussion* under *Propora speciosa*, pp. 60, 61).

The other genera included in the synonymy have been discussed in one or more recent studies, but a few points require further discussion. *Mcleodea*, from the Aleman Formation of Texas (Upper Ordovician, Maysvillian–Richmondian; Sweet, 1979, fig. 4), is very similar to *Propora*. It has a coenenchyme that is almost tubular where tabularia are closely spaced, however, and has walls that are composed of the lateral edges of coenenchymal dissepiments in some places. Young and Noble (1990b, p. 188) noted that some specimens of *Propora exigua* (Billings) from the Lower Silurian of northern New Brunswick have coenenchymes of similar character. Corallite walls composed of the lateral edges of coenenchymal dissepiments occur in *Propora* sp. A from the Sexton Creek Limestone of southern Illinois (lower Lower Silurian, Lower? Llandovery) (Pl. 8, fig. 2) and in *Propora americana* (Milne-Edwards and Haime) from the Lower Silurian of northern New Brunswick (Young and Noble, 1990b, fig. 6.4). For these reasons, we tentatively synonymize *Mcleodea* with *Propora*.

Young and Noble (1990b, pp. 187, 188) considered *Rotalites* Leleshus (1974, p. 97), from the Upper Silurian of Tadzhikistan, to be a junior synonym of *Propora*. The dissepiment-like longitudinal folds that occur in the walls of *Rotalites* are, however, very distinctive. We recognize it as a separate genus, almost certainly derived from *Propora*.

Propora thebesensis (Foerste, 1909)

Plate 1, figures 1–11; Plate 2, figures 1–12;
Plate 3, figures 1–11; Plate 4, figures 1–10

Heliolites affinis Billings, 1865, pp. 427, 428 [*partim*]; 1866, pp. 5, 6 [*partim*].

Lyellia affinis (Billings, 1865). Lambe, 1899, pp. 84, 85 [*partim; non* pl. 5, figs. 1, 1a]; Twenhofel, 1928, p. 133 [*partim*].

[?] *Propora conferta* Milne-Edwards and Haime, 1851. Lindström, 1899, pp. 93, 94 [*partim*], pl. 9, figs. 11, 12 [*non* pl. 8, figs. 32–39, pl. 9, figs. 1–10, 13–23]; Bolton, 1980, p. 20, pl. 2.4, figs. 1–3, 9, 10, pl. 2.5, fig. 7.

Lyellia thebesensis Foerste, 1909, p. 95, pl. 4, figs. 69a, 69b; Savage, 1913, pp. 66, 67, pl. 3, figs. 6, 7; 1917, pp. 116, 117, pl. 5, figs. 6, 7.

[*cf.*] *Propora* cfr. *magnifica* Počta, 1902. Ozaki, 1934, p. 67, pl. 10, figs. 9, 10, pl. 11, fig. 1.

[*cf.*] *Propora yabei* Ozaki, 1934, pp. 67, 68, pl. 11, figs. 2, 3.

[*cf.*] *Propora conferta* var. *tunicata* Sokolov, 1950b, p. 229, pl. 7, figs. 1, 2.

[*cf.*] *Propora cancellatiformis* Sokolov, 1950b, pp. 230, 231, pl. 7, figs. 3, 4, pl. 8, figs. 1, 2.

[?] *Lyellia thebesensis paucivesiculosa* Bolton, 1957, pp. 64, 65, pl. 6, figs. 1–7.

Propora conferta Milne-Edwards and Haime, 1851. Dixon, 1974, pp. 570–580, figs. 5, 6, pl. 1, figs. 1–9, pl. 2, figs. 1–9; Bolton, 1981a, pl. 1, figs. 6, 7, pl. 2, figs. 6, 7, pl. 3, figs. 1, 2, pl. 8, figs. 13, 14 [*non* pl. 9, fig. 1, pl. 11, figs. 1, 2].

Propora thebesensis (Foerste, 1909). Elias and Young, 1992, figs. 3c, 3d; Young and Elias, 1993, pl. 1, figs. 5–10.

Diagnosis.—*Propora* with smooth-walled or crenulate tabularia, adult tabularium diameters usually 0.9–1.4 mm; tabularium area about 30–70% of corallite area. Where present, septa are composed of thickened ridges; discrete spines absent. Coenenchymal dissepiments globose; coenenchyme lacks vertical rods and plates.

Description of coralla.—Coralla are of low and high bulbous and domical, and low columnar growth forms (Table 14; Pl. 2, fig. 11, Pl. 3, figs. 4, 8). Sizes of coralla range from 10–147 mm wide and 11–73 mm high; most are small.

In transverse section, tabularia are smooth-walled and subcircular (Pl. 2, fig. 8), slightly crenulate (Pl. 1, fig. 6, Pl. 3, figs. 1, 5, Pl. 4, fig. 4), or with marked trabecular thickenings that rarely develop exothecal extensions (Pl. 1, figs. 1, 5, 7, Pl. 2, figs. 5, 6). Adult tabularia commonly have diameters of 0.9–1.4 mm (Table 15). Tabularia are close-spaced to very close-spaced; tabularium area is usually 45–65% of corallite area (Table 15). Where tabularia are closely spaced, tabularium shape may become subpolygonal (Pl. 2, fig.

Table 14.—Growth forms of coralla by species and collection intervals in the east-central United States.

species	*growth forms*						
section-intervals (n = no. of coralla)	*bulbo-columnar*	*domico-columnar*	*high bulbous*	*high domical*	*low bulbous*	*low domical*	*tabular*
Propora thebesensis							
23-2 (n = 6)	—	—	—	3	1	2	—
31-1 and 31-1b (n = 10)	7	—	1	—	—	2	—
14-1 (n = 10)	2	1	3	2	2	—	—
15-1 (n = 4)	—	—	3	1	—	—	—
16-2 (n = 1)	—	—	1	—	—	—	—
other (n = 3)	1	—	—	1	—	1	—
all (n = 34)	10	1	8	7	3	5	0
Propora savagei							
20-1 (n = 1)	1	—	—	—	—	—	—
31-1 and 31-1b (n = 2)	—	—	2	—	—	—	—
all (n = 3)	1	0	2	0	0	0	0
Halysites alexandricus							
23-2 (n = 1)	—	—	1	—	—	—	—
31-1 and 31-1b (n = 2)	—	—	—	—	1	1	—
37-1 (n = 1)	—	—	—	—	—	1	—
all (n = 4)	0	0	1	0	1	2	0
Paleofavosites subelongus							
31-1 and 31-1b (n = 1)	—	—	—	—	—	1	—
14-1 (n = 24)	2	—	7	6	3	6	—
15-1 (n = 4)	—	—	2	—	1	1	—
16-1 (n = 1)	—	—	—	1	—	—	—
18-1 and 18-2 (n = 2)	—	1	1	—	—	—	—
32-1z (n = 23)	—	1	2	11	1	8	—
all (n = 55)	2	2	12	18	5	16	0
Paleofavosites sp. cf. *P. subelongus*							
32-1c (n = 2)	—	—	1	—	—	1	—
Paleofavosites adaensis							
35-1 (n = 2)	—	—	—	—	—	—	2
Paleofavosites sp. A							
5-2 and 6-1 (n = 3)	—	—	—	—	—	2	1

1, Pl. 3, figs. 6, 9, Pl. 4, fig. 6); in extreme cases the character of growth mimics that of *Favosites*. In longitudinal section, tabularia are straight in the axial part of the corallum but are often strongly curved in more marginal parts (Pl. 2, fig. 9, Pl. 3, fig. 4). In coralla with close spacing of tabularia, adjacent individuals may have walls in contact for a substantial portion of their length (Pl. 3, fig. 10, Pl. 4, fig. 7).

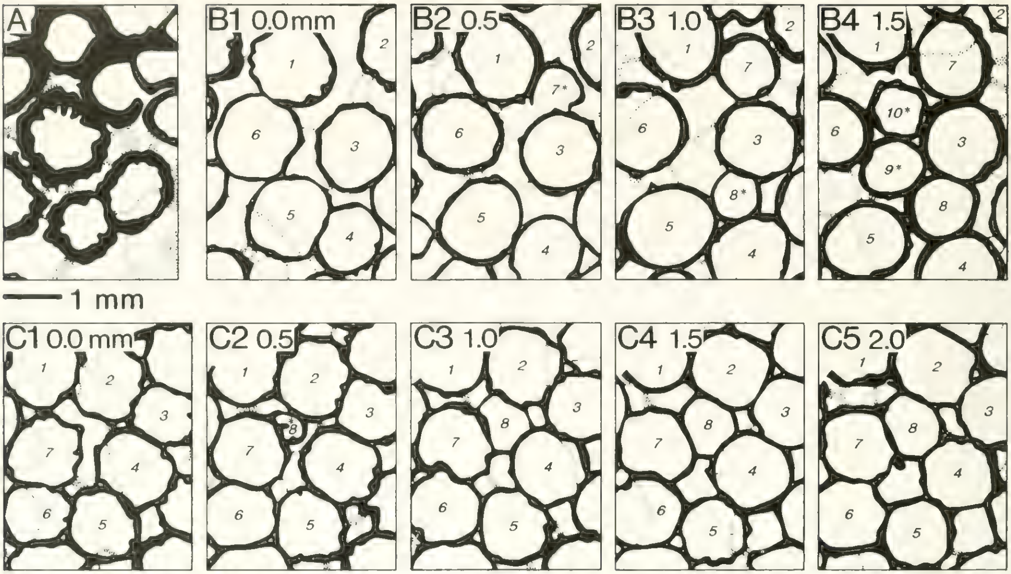
Walls are thin and smooth, or have slight to pronounced trabecular thickening at septa. Wall thickness is commonly 0.06–0.10 mm (Table 15). Septa are variably developed, absent to 12 pronounced thickened ridges; trabecular thickening varies cyclomorphically (Pl. 1, figs. 5, 10). In transverse section, septal thickening may be variably developed within a single corallite (Pl. 2, fig. 6). Septal length is commonly 0–25% of tabularium radius (Table 15). Discrete septal spines are absent; small ragged extensions are very rarely present at inner edges of trabeculae.

Tabulae are of moderate thickness; flat, wavy, or slightly convex or concave (Pl. 2, figs. 4, 9); rarely strongly concave or V-shaped (Pl. 1, fig. 2). Tabulae are usually complete (Pl. 4, fig. 7), rarely incomplete (Pl. 4, fig. 8). Tabulae are widely spaced (Pl. 2, fig. 9, Pl. 3, fig. 10), averaging about eight in 5 mm (Table 15); rarely closely spaced (Pl. 1, fig. 11). Spacing and thickening of tabulae show only slight cyclomorphic variation, even where thickening of septal trabeculae is extremely variable.

In longitudinal section, coenenchyme is composed of moderately widely spaced, globose dissepiments, averaging about 15 in 5 mm; about twice as many dissepiments as corallite tabulae per unit of vertical distance (Table 15). Dissepiments are thin, but are slightly thickened near corallite walls; they may show slight cyclomorphic thickening (Pl. 1, fig. 2). Dissepiments are usually regularly arranged, but may be irregular in some parts of a corallum. Where tabularia are very

Table 15.—Biometric data for proporids from the east-central United States. *TaD* = tabularium diameter, *TaA* = tabularium area, *CoA* = corallite area, *WT* = wall thickness, *LS* = length of septa, *Ta5* = number of tabulae in 5 mm, *Di5* = number of coenenchymal dissepiments in 5 mm, *TC* = thickness of cycles; s.d. = standard deviation, c.v. = coefficient of variation.

species	*parameters*									
data	*TaD*	*TaA*	*CoA*	*TaA:CoA*	*WT*	*LS*	*Ta5*	*Di5*	*Ta5:Di5*	*TC*
Propora thebesensis										
mean	1.13 mm	1.01 mm^2	1.88 mm^2	0.54	0.080 mm	7%	7.7	14.7	0.51	–
range of colony means	0.88–1.46 mm	0.61–1.67 mm^2	1.25–2.63 mm^2	0.35–0.71	0.057–0.133 mm	0–28%	4.4–13.3	10.6–20.5	0.32–0.84	–
s.d. of colony means	0.11 mm	0.21 mm^2	0.31 mm^2	0.09	0.016 mm	8%	1.7	2.6	0.11	–
c.v. of colony means	9.7	20.8	16.5	16.7	20.0	114.3	22.1	17.7	21.6	–
minimum	0.18 mm	–	–	–	0.050 mm	–	3	8	–	–
maximum	1.65 mm	–	–	–	0.350 mm	–	18	30	–	–
mean intracolony c.v.	10.7	–	–	–	22.3	–	14.0	14.8	–	–
no. of coralla studied	84	84	67	67	48	62	72	37	37	–
Propora savagei										
mean	1.62 mm	2.11 mm^2	4.63 mm^2	0.42	0.167 mm	27%	7.2	13.1	0.56	–
range of colony means	0.98–2.06 mm	0.75–3.33 mm^2	1.75–6.90 mm^2	0.30–0.54	0.085–0.258 mm	16–44%	5.4–11.4	9.6–19.3	0.47–0.69	–
s.d. of colony means	0.29 mm	0.71 mm^2	1.52 mm^2	0.08	0.065 mm	9%	2.1	3.9	0.10	–
c.v. of colony means	17.9	33.6	32.8	19.0	38.9	33.3	29.2	29.8	17.9	–
minimum	0.45 mm	–	–	–	0.050 mm	–	3	8	–	–
maximum	2.10 mm	–	–	–	0.300 mm	–	14	23	–	–
mean intracolony c.v.	9.0	–	–	–	21.0	–	15.0	13.2	–	–
no. of coralla studied	15	15	11	11	5	8	10	5	5	–
Propora speciosa										
mean	2.49 mm	4.87 mm^2	15.52 mm^2	0.31	0.213 mm	64%	5.4	8.8	0.59	–
range of colony means	2.34–2.60 mm	4.30–5.34 mm^2	13.30–16.78 mm^2	0.27–0.37	0.181–0.225 mm	56–75%	4.8–5.8	7.8–10.3	0.54–0.64	–
s.d. of colony means	0.11 mm	0.44 mm^2	1.53 mm^2	0.04	0.019 mm	10%	0.5	1.1	0.05	–
c.v. of colony means	4.4	9.0	9.9	12.9	8.9	15.6	9.3	12.5	8.5	–
minimum	1.75 mm	–	–	–	0.125 mm	–	4	7	–	–
maximum	2.90 mm	–	–	–	0.300 mm	–	7	13	–	–
mean intracolony c.v.	8.6	–	–	–	19.7	–	15.6	11.7	–	–
no. of coralla studied	5	5	4	4	5	3	3	4	3	–
Propora sp. aff. *P. affinis*										
mean	1.17 mm	1.08 mm^2	2.84 mm^2	0.38	0.064 mm	12%	10.5	13.5	0.78	4.0 mm
minimum	0.85 mm	–	–	–	0.025 mm	–	8	11	–	2.1 mm
maximum	1.30 mm	–	–	–	0.100 mm	–	15	18	–	5.3 mm
intracolony c.v.	6.8	–	–	–	11.2	–	17.0	13.7	–	–
no. of coralla studied	1	1	1	1	1	1	1	1	1	1
Propora sp. A										
mean	2.56 mm	5.17 mm^2	25.84 mm^2	0.20	0.140 mm	78%	13.2	10.6	1.25	–
minimum	1.85 mm	–	–	–	0.125 mm	–	10	8	–	–
maximum	3.10 mm	–	–	–	0.175 mm	–	13	14	–	–
intracolony c.v.	13.0	–	–	–	5.3	–	15.2	17.9	–	–
no. of coralla studied	1	1	1	1	1	1	1	1	1	–



Text-figure 12.—Transverse sections illustrating astogeny and corallite increase in *Propora thebesensis*. **A**, Earliest growth stage of a corallum, showing group of similar thick-walled corallites; USNM 485701, Section-interval 23-2 (Lawrence Quarry). **B1–B4**, Serial sections showing corallite increase in axial part of a corallum having broad tabularium spacing; USNM 459087, Section-interval 23-2 (Lawrence Quarry). **C1–C5**, Serial sections showing corallite increase in axial part of a corallum having close tabularium spacing; USNM 459076, Section-interval 16-2 (Clinton Spring) (see also Pl. 3, figs. 8–11). Corallite walls and septa are solid, tabulae and dissepiments are stippled; scale bar is shown. For B and C, heights in mm are above an arbitrary datum within the mature part of each corallum; numbers in italics represent individual corallites; an asterisk indicates the first appearance of a particular corallite.

closely spaced, dissepiments appear as flat, horizontal plates (Pl. 3, fig. 7, Pl. 4, figs. 2, 5, 7); where tabularia are widely spaced, dissepiments become more broadly domed (Pl. 1, fig. 2, Pl. 2, fig. 4). In some places the outer edges of thickened septal trabeculae appear as small nodes or vertical plates on the upper surfaces of dissepiments (Pl. 1, fig. 2). In transverse section, dissepiments are thin and sparsely distributed (Pl. 1, figs. 1, 5). Where cyclomorphic variation in thickness of elements is pronounced, extreme thickening of septal structures may replace the coenenchyme with a dense trabecular mass between adjacent tabularia (Pl. 1, fig. 11).

Astogeny and corallite increase.—Descriptions are based principally on two serial-sectioned coralla (USNM 459076, 459087) and six serial-sliced coralla (USNM 459075, 485701, 485711, 485712, 485741, 485753). Other specimens are used for comparison.

The earliest growth stages are recognized in three coralla. In each of these, the protocorallite cannot be distinguished. Rather, a small group of up to 10 similar, closely spaced corallites occurs at the absolute base of the corallum (Text-fig. 12A); these corallites are subvertical to divergent, arising from a plate-like holotheca. In two of the three coralla, the holothecae are based on tabular stromatoporoids. The character of the initial corallites varies between coralla; they can be thin-walled or thick-walled, and have pronounced septal trabeculae (Text-fig. 12A) or are smooth-walled and almost aseptate.

Spacing of tabularia is commonly less dense above the basal part of a corallum, but in some specimens it remains very dense. Wall thickness within a corallite commonly changed during growth; if initial stages are thin-walled and aseptate, septal trabeculae may appear at 1.5–2.0 mm above the corallite's base. Cyclomorphic variation in thickening and spacing of elements is generally slight (see *Description of coralla,* above). In many coralla, some corallites extend from the base to the upper growth surface. Skeletal elements may be thick and densely spaced at the upper surface of a corallum, or they may be identical to those occurring below.

Corallite increase is coenenchymal; there are two modes of initiation depending on density of tabularium spacing. Where spacing is broad, large tabularia that are of nearly adult size were initiated on the upper surfaces of coenenchymal dissepiments, with corallite walls based directly on the dissepiments (Pl. 1, fig. 2, Pl. 2, fig. 4). In transverse section, new tabularia initiated in such settings are smooth-walled and subcircular (Text-fig. 12B1–B4; Pl. 1, fig. 3), or may possess large, thick septa before the corallite wall is complete (Pl. 1, fig. 4). New tabularia in broadly spaced settings expanded rapidly (Text-fig. 12B2–B4).

Where spacing of tabularia is close, small new tabularia were initiated against the outer walls of older individuals only where space permitted (Text-fig. 12C1–C5). At the base of each initiate there is a gradual transition in character of horizontal elements, from coenenchymal dissepiments to tabulae (Pl. 3, figs. 7, 10, 11, Pl. 4, fig. 7). In transverse section, new tabularia in close-spaced settings are smooth-walled or crenulate and are subpolygonal, with their sides compressed by the walls of adjacent individuals. Initiates in such settings expanded slowly (Text-fig. 12C2–C5).

The two modes of initiation can occur in different parts of a single corallum. The boundary between modes occurs where tabularium area is about 50–60% of corallite area. Bursts of increase are sometimes concentrated in skeletal bands showing cyclomorphically close vertical spacing of elements. Increase may be common up to the very top of a corallum.

In many coralla there are significant differences between the axis (area of vertical and subvertical growth) and the margins (area of more lateral growth). Tabulae are more broadly spaced in the axis than in the margins; thickening of elements is similar between the two areas, and cyclomorphic bands are continuous between the two (Pl. 3, fig. 8). Tabularia are closer together in the axis than in the margins in many coralla. There was more increase in the axis, so corallites there tend to have slightly smaller mean tabularium diameters. The relative dimensions of the axis and margins reflect corallum growth patterns and the shape of the growth surface. Relatively narrow margins are associated with more vertical growth that produced tall coralla with relatively small growth surfaces (Pl. 3, fig. 4). Marginal corallites in such coralla were often short-lived. Relatively wider margins occur in coralla that have broader growth forms (Pl. 3, fig. 8).

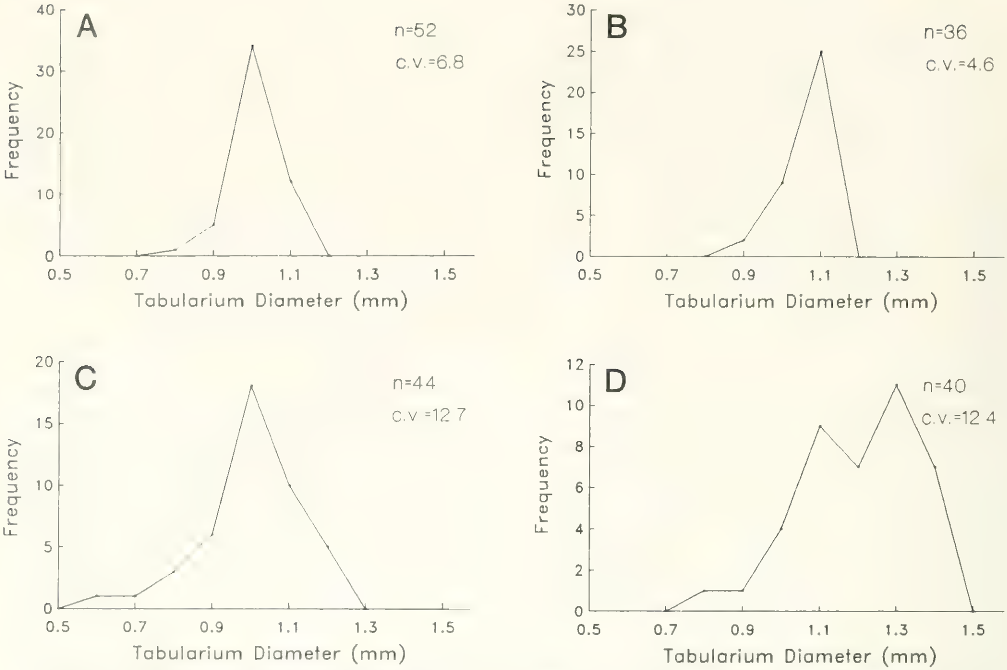
Sediment inclusions representing partial mortality of the colony surface occur in many specimens. Above these inclusions, new corallites of adult or nearly adult size were initiated across the surface of a thin holothecal layer (Pl. 2, fig. 7). These corallites are separated by coenenchymal dissepiments that are densely spaced, but of normal form. Lateral to such an inclusion, corallites in a cyclomorphically dense band may show constriction followed by rejuvenescence (Pl. 2, fig. 2, Pl. 4, fig. 3). In one corallum, the presence of an algal crust on an area of partial mortality suggests that this surface was exposed for a significant period of time prior to regeneration. Regeneration may be associated with a change in growth direction indicative of colony reorientation. Coralla were able to successfully surround and overgrow large particles deposited on their growth surfaces (Pl. 1, fig. 8).

Microstructure.—Corallite walls were produced principally by the joining together of adjacent septal trabeculae. This is most obvious where the trabeculae are thickened; the adjacent septal trabeculae commonly have thin connecting walls with which they are continuous (Pl. 1, fig. 9, Pl. 2, fig. 6). Even where septa are absent, the walls appear to be composed of trabeculae. Under polarized light, a line can be observed passing through the axes of thickened trabeculae and continuing along the wall between septa. Where the septal trabeculae are strongly thickened, the axial edges of trabeculae may be irregular and ragged, but no discrete spines are present. The trabeculae of adjacent, close-spaced corallites may coalesce without a clearly defined suture. Where corallites are closely spaced and trabeculae are thickened, pore-like structures may appear in the walls (Pl. 3, fig. 11).

Microstructure of tabulae and coenenchymal dissepiments is generally indistinct; tabulae and dissepiments are darker in color than the pale trabeculae of corallite walls (Pl. 1, fig. 9). Dissepiments are often embedded in corallite walls more deeply than are tabulae, which are attached to adaxial edges of wall trabeculae (Pl. 2, fig. 10).

Intraspecific variation.—Coralla show a high degree of variability in a number of morphologic characters, including size and spacing of tabularia, and features that are related to thickening of skeletal elements. This variability is pronounced, both within and between coralla and localities.

Tabularium size-frequency distributions show variation within and between coralla. Transverse sections from some coralla have low intracorallum variability in tabularium diameter; distributions for such specimens are unimodal, with slight negative skewness (Text-fig. 13A, B). Coralla with high intracorallum variability in tabularium diameter show two types of tabularium size-frequency distributions. Some (*e.g.*, Text-fig. 13C) are similar to the distribution seen in less variable specimens, but have a larger number of small individuals. Others show bimodal frequency distributions (Text-fig. 13D). Greater variability of tabularium diameters is most common in coralla with dense tabularium spacing and subpolygonal tabularia (*e.g.*, Pl. 3,

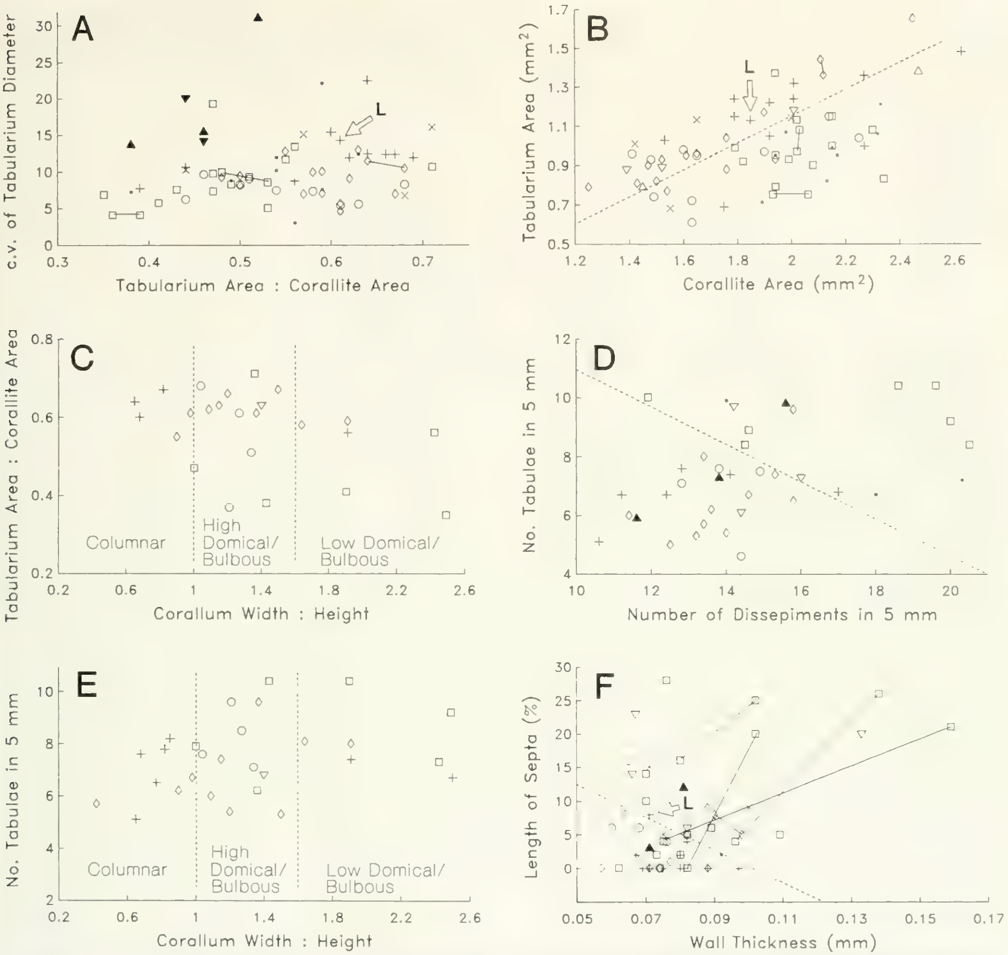


Text-figure 13.—Tabularium size-frequency distributions for selected coralla of *Propora thebesensis*. **A**, USNM 485706a, Section-interval 23-2 (Lawrence Quarry). **B**, USNM 485756, Section-interval 14-1 (Higginbotham Farm). **C**, USNM 485739, Section-interval 14-1 (Higginbotham Farm). **D**, USNM 485716, Section-interval 31-1 (Thebes North). Each graph represents a single transverse section; n = number of tabularia, c.v. = coefficient of variation.

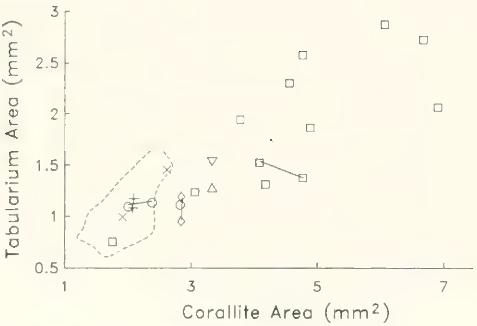
figs. 6, 9); this observation is supported by a graph of variability of tabularium diameter *versus* corallite packing for transverse sections from all measured coralla (Text-fig. 14A). This holds for intervals from which large collections were available, such as Section-interval 23-2 (Lawrence Quarry), and Section-intervals 31-1 and 31-1b (Thebes North). Specimens from two of the small collections, however, are radically different. Coralla from the Gale Section and from 5 km south of Clarksville, Missouri, have wide-spaced tabularia that are highly variable in size. Possible reasons for a general correlation between density of corallite packing and variability of tabularium diameter are considered elsewhere (see *Propora thebesensis,* p. 35).

A strong positive correlation is observed in a graph of mean tabularium area *versus* mean corallite area in transverse sections (Text-fig. 14B). This relationship is not 1:1; rather, as tabularia became larger they also tended to become more closely spaced. Specimens from each of the localities for which large collections were available show considerable variability in these features, but tend to be concentrated in one part or another of the graph. There is some evidence that these characters of size and spacing are tied to colony growth form. Those intervals in which tabularia are relatively densely spaced, such as Section-intervals 31-1 and 31-1b, and Section-interval 14-1 (Higginbotham Farm), are the ones in which taller growth forms predominate. Where tabularia are broadly spaced (Section-interval 23-2) lower forms are most common (compare Text-figs. 10 and 14B; see Tables 10, 11). The correlation between form and packing is less clear on a graph for individual coralla (Text-fig. 14C). A general trend can be distinguished, but the broad spread of points suggests that styles of growth varied (see *Astogeny and corallite increase,* above; *Growth Form,* p. 29; *P. thebesensis,* p. 35).

Vertical spacings of tabulae and of coenenchymal dissepiments show a general linear relationship (Text-fig. 14D); these characters also vary with locality and



Text-figure 14.—Intercorallum variation in morphologic characters of *Propora thebesensis* from the east-central United States. **A**, Relationship between coefficient of variation (c.v.) of tabularium diameter and density of tabularium spacing (mean tabularium area as a proportion of mean corallite area) for transverse sections from 67 coralla. **B**, Relationship between mean tabularium area and mean corallite area for transverse sections from 69 coralla. **C**, Relationship between density of tabularium spacing and generalized growth form (corallum width as a proportion of corallum height) for 24 coralla. **D**, Relationship between number of tabulae and number of dissepiments in unit 5 mm for longitudinal sections from 37 coralla. **E**, Relationship between number of tabulae in unit 5 mm and generalized growth form for 28 coralla. **F**, Relationship between length of septa as a percentage of tabularium radius and mean wall thickness for transverse sections from 47 coralla. Each data point represents a single thin section; solid lines connect sections from different parts of a single corallum; L = USNM 84863b (lectotype). Arbitrary dashed lines in B, D, and F were used to derive proportions shown in Table 11. Terms for corallum growth form in C and E are defined in *Growth Form* under *The Edgewood Colonial Corals*. Symbols for Sections and Section-intervals: □ 23-2 and 23-2a (Lawrence Quarry); + 31-1 and 31-1b (Thebes North); ▼ Gale Section; × 18-3 and 18-4 (Kissenger); ▲ 5 km south of Clarksville, Missouri; ▽ 16-1 and 16-2 (Clinton Spring); ◇ 14-1 (Higginbotham Farm); ○ 15-1 (Calumet); △ 32-1c (Thomson East); ■ all other Section-intervals.



Text-figure 15.—Comparison of selected species of *Propora:* relationship between mean tabularium area and mean corallite area on transverse sections. Data points are for individual coralla except as otherwise stated; solid lines connect thin sections from single coralla. A dashed line surrounds the field of distribution for 69 coralla of *P. thebesensis* from the east-central United States. Symbols for other species: □ *P. savagei;* east-central United States; n (number of coralla) = 11; ◇ *Propora* sp. aff. *P. affinis;* east-central United States; n = 1; ○ *P. thebesensis paucivesiculosa;* Manitoulin Formation, southern Ontario; n = 2; ▽ *P. affinis;* Gun River Formation, Anticosti Island, Québec; GSC 2340, 2340a (one syntype); + *P. conferta;* Ellis Bay Formation, Anticosti Island, Québec; the two data points represent means for specimens from Pointe Laframboise (n = 179) and all other localities (n = 59) (data from Dixon, 1974, table 3); × *P. conferta;* Grande Coupe beds, Matapédia Group, near Percé, Québec; n = 3; △ *Propora* sp. A of Bolton (1980); Honorat Group, north of Carleton, Québec; n = 1.

with growth form. Coralla from Section-intervals 31-1, 31-1b, and 14-1, where tall forms are most common, have tabulae and dissepiments with wider vertical spacings than do those from Section-interval 23-2, where lower forms are dominant (see Tables 10, 11). As was the case for packing of tabularia, this correlation is stronger when examined by locality (Text-fig. 14D) than when plotted for individual coralla (Text-fig. 14E). For further discussion on the relationship between growth form and vertical spacing of elements, see *Growth Rate* (p. 31).

Thickening of walls and development of septa are extremely variable (Text-fig. 14F). Skeletal elements in coralla from Section-interval 23-2 are commonly more strongly thickened than those in specimens from other localities. There is overlap, however, and measurements from different parts of individual specimens from Section-interval 23-2 indicate that intracolony variation can be nearly as great as the intraspecific variability.

General comparisons of characters at the major localities are presented elsewhere (see *Propora thebesensis,* p. 35).

Discussion.—Foerste (1909) based *Lyellia thebesensis* on material collected at Section 31 (Thebes North). He illustrated two coralla, which we designate as the lectotype (USNM 84863b; see Pl. 3, figs 1, 2) and paralectotype (USNM 84863a; see Pl. 3, fig. 3) of *Propora thebesensis.* The lectotype is better preserved than are most specimens from this locality, and shows a degree of cyclomorphic variation that records much of the range of intraspecific variability. Most numerical characters of this specimen are near the species mean: TaD = 1.20 mm, CoA = 1.85 mm^2, WT = 0.071 mm (thickened) and 0.058 mm (unthickened), LS = 15% (thickened) and 0% (unthickened) (compare with Table 15).

Lyellia thebesensis from the type locality was also described and illustrated by Savage (1913, 1917). The corallum he photographed (Savage, 1913, pl. 3, fig. 7; 1917, pl. 5, fig. 7) is apparently lost; the specimen labelled as Savage's hypotype (UI X-908; see Pl. 2, figs. 11, 12) is externally similar but is not identical. Many coralla that we have studied from the type locality are near one end of the spectrum of variation of *P. thebesensis* (see *Intraspecific variation,* above), but they are clearly conspecific with all other material of this species. Two other species included in this study, *Propora savagei* and *Propora* sp. aff. *P. affinis,* have some close similarities to *P. thebesensis* (see Text-fig. 15); the differences and possible relationships are discussed under those two species.

The only material previously described as *P. thebesensis* from outside the east-central United States is from the Manitoulin Formation of the Cataract Group in southern Ontario (lower Lower Silurian, Lower Llandovery, Rhuddanian; Barnes and Bolton, 1988, p. 252; Brett *et al.,* 1991, fig. 5). This material was designated as *Lyellia thebesensis paucivesiculosa* by Bolton (1957). We examined the following material: ROM 7490 (Bolton, 1957, pl. 6, fig. 4), 7491(783CL) (holotype; Bolton, 1957, pl. 6, figs. 2, 3, 5–7), upper biohermal beds, ROM 7474a(766CL), 7474b(766CL), 29542, collected by H. G. Way, Bidwell Township, Manitoulin Island, Ontario; GSC 11066 (Bolton, 1957, pl. 6, fig. 1), collected by T. E. Bolton in 1950, southeast quarry of Owen Sound, Ontario.

Bolton's holotype of *L. thebesensis paucivesiculosa* has tabularia with a mean diameter of 1.17 mm, tabularium area averaging 50% of corallite area, thin walls, and small, globose coenenchymal dissepiments. These features, and those of most other specimens of *L. thebesensis paucivesiculosa,* are consistent with characters of *P. thebesensis.* One corallum of the former (ROM 7474b), however, has slightly larger tabularia than is common in specimens from the east-central United States, and another (GSC 11066) has tabularia that are much more widely spaced (Text-fig.

15). For these reasons, material from the Manitoulin Formation is questionably considered conspecific with *P. thebesensis*, and probably represents a distinct geographic subspecies as recognized by Bolton (1957).

Propora thebesensis is a member of a group of Late Ordovician and Early Silurian species belonging to *Propora* that have similar tabularium sizes (typically in the range of 1–2 mm), septa that may have trabecular thickening but lack spines, and coenenchymes that do not have well-developed vertical rods or plates. Other members of this group have been commonly assigned to *Propora affinis* and *Propora conferta*, but the high intraspecific variability of *P. thebesensis* and the other taxa makes recognition of species boundaries difficult. It is clear that at least some of the differences between species are related to stratigraphic position and may be due to phyletic evolution, but geographic variation may also be a factor; detailed analysis of variation in other regions is needed.

Specimens that are similar to *P. thebesensis* occur in the uppermost Ordovician (Gamachian) to lower Lower Silurian (Llandovery) on Anticosti Island, Québec, in units ranging from the Ellis Bay Formation to the Chicotte Formation. These proporids have previously been assigned to either *P. affinis* or *P. conferta*. *Propora thebesensis* is not conspecific with the type material of either species, but it is conspecific with some specimens from Anticosti that have been assigned to both species in the past. The names *affinis* and *conferta* have long and complex histories, and a brief discussion of each is necessary so that species relationships can be put into context.

Heliolites affinis was proposed by Billings (1865) to include a variety of material of different ages from several parts of Anticosti Island. We examined a syntype (GSC 2340, 2340a) collected by J. Richardson in 1856 from about 5 km west of the mouth of Jupiter River. This specimen is from the Gun River Formation (Middle Llandovery, lower Aeronian; Barnes, 1988, fig. 2) (see Dixon, 1974, p. 578; Bolton, oral commun., 1993). It has a tall bulbous growth form, a mean tabularium diameter of 1.40 mm (measured on external surface), and tabularium area averaging 46% of corallite area. These characters are consistent with those of *P. thebesensis*, but this specimen differs from the latter species by having a larger mean corallite area of 3.33 mm^2 (see Text-fig. 15) and it appears to have broad coenenchymal dissepiments. Billings (1866) later republished his description of this species, and other early workers, including Lambe (1899) and Twenhofel (1928), used the name *affinis* and followed his concept of it as a widely occurring species on Anticosti.

Propora conferta was first described, but not illustrated, by Milne-Edwards and Haime (1851, p. 225) from Borkholm (probably Upper Ordovician, Ashgill, F_{II}, Porkuni Stage; Twenhofel, 1916, pp. 293, 306; Rõõmusoks, 1960, table 1) and Chavli, Estonia (probably not *in situ* according to Lindström, 1899, p. 93). The type specimens, as described and illustrated by Lindström (1899, pp. 93, 94, pl. 8, figs. 32–34, 37–39), differ from *P. thebesensis* by having larger tabularia with diameters of about 1.75–2.0 mm, often broad coenenchymal dissepiments, and sometimes very densely spaced tabulae. Lindström (1899, pp. 93, 94) was the first to consider *P. affinis* to be a junior synonym of *P. conferta*. The synonymization of these two species has been followed more recently by Dixon (1974) and Bolton (1981a).

The available illustrations and descriptions of *P. affinis/conferta* from Anticosti Island indicate that the older specimens, from the Ellis Bay Formation (Gamachian to possibly Lower Llandovery, lowermost Rhuddanian; Melchin *et al.*, 1991, p. 1861) and the Becscie Formation (Rhuddanian; Barnes, 1988, fig. 2), are so similar to *P. thebesensis* that they must be considered conspecific with it; changes in character that are apparently evolutionary prevent such an assignment for material from younger formations. Variation in specimens from member 7 at the top of the Ellis Bay Formation at a number of localities has been documented by Dixon (1974; unit referred to as member 6 therein). These specimens have a variety of growth forms, subcircular tabularia with a mean diameter of 1.2 mm, variable but generally close tabularium spacing with tabularium area averaging 52% of corallite area, sometimes thickened septal trabeculae, and globose coenenchymal dissepiments. Their overall range of variation is very similar to that of *P. thebesensis* from the east-central United States (see Text-fig. 15); the only difference is that tabularia in the Anticosti material are apparently never so densely spaced that they become subpolygonal.

Material identified as *P. conferta* from the Ellis Bay Formation at several localities has also been illustrated by Bolton (1981a, pl. 1, figs. 6, 7, pl. 2, figs. 6, 7, pl. 3, figs. 1, 2); it has characters consistent with those of *P. thebesensis*. The corallum illustrated by Lindström (1899, pl. 9, figs. 11, 12) from Junction Cliff is probably from the lower Ellis Bay Formation (see Barnes *et al.*, 1981, p. 8); it has somewhat wider spaced tabularia and broader coenenchymal dissepiments than is typical for *P. thebesensis*. Specimens from the overlying Becscie Formation, as illustrated by Bolton (1981a, pl. 8, figs. 13, 14), are very similar to *P. thebesensis* from the Keel Formation at Section 23 (Lawrence Quarry) (*e.g.*, USNM 458777; Pl. 1, figs. 4–9). Material has also been illustrated and described from the younger Gun River Formation, Jupiter Formation (upper Aeronian–

Telychian) and Chicotte Formation (Upper Llandovery, Telychian; Barnes, 1988, fig. 2) on Anticosti Island. This includes a syntype of *P. affinis* (GSC 2340, 2340a; see above) and the specimens of Bolton (1981a, pl. 9, fig. 1, pl. 11, figs. 1, 2); tabularia are typically larger and/or more widely spaced than those of *P. thebesensis*. Intraspecific variation in these younger units has not been analyzed in detail, however, and the illustrated material may not be typical.

Coralla identified as *P. conferta* from the Grande Coupe beds of the Matapédia Group near Percé, Québec (Upper Ordovician, Ashgill, pre-Hirnantian; Lespérance *et al.*, 1987, fig. 4), were described and illustrated by Bolton (1980; White Head Formation therein). We examined the following material: GSC 53528 (Bolton, 1980, pl. 2.4, fig. 1, pl. 2.5, fig. 7), 53529 (Bolton, 1980, pl. 2.4, figs. 2, 3), 53530 (Bolton, 1980, pl. 2.4, figs. 9, 10), collected by G. W. Sinclair in 1956, Grande Coupe, Québec. These hypotypes are very similar to *P. thebesensis* from the east-central United States. They have mean tabularium diameters of 1.12–1.36 mm, tabularium area averaging 41–56% of corallite area, thin walls, flat or slightly concave tabulae, and globose coenenchymal dissepiments. Nevertheless, since one of them has much more widely spaced tabularia than do specimens of *P. thebesensis* with comparable tabularium areas (Text-fig. 15), we consider them to be questionably conspecific with the latter. As they may be somewhat older than the United States material, they may represent a stratigraphically distinct subspecies. Bolton (1980, p. 14, pl. 2.2, figs. 1, 2) also described and illustrated a specimen identified as *Propora* sp. A, from the Upper Ordovician Honorat Group north of Carleton, Québec. We examined this corallum, collected by J. E. Béland and W. H. Poole in 1979 (GSC 53514). It is similar to *P. thebesensis*, having circular tabularia with a mean diameter of 1.27 mm, tabularium area averaging 38% of corallite area, and walls that appear to be of moderate thickness. Its poor preservation, however, makes detailed comparisons impossible.

Corals from two other areas of North America are similar to *P. thebesensis*. Stearn (1956, p. 72, pl. 6, fig. 3) identified *Lyellia affinis* from the Fisher Branch, East Arm, Cedar Lake, and possibly Atikameg formations of southern Manitoba (lower–upper Lower Silurian, upper Rhuddanian–Lower Wenlock; Johnson and Lescinsky, 1986, fig. 6). He described it as having generally smooth-walled tabularia with diameters (outside?) of about 1.5 mm; tabularia are in contact or separated by distances up to one-half their diameter. The only illustration of this material is an external view of a corallum, so it is difficult to determine more details. Laub (1979, pp. 332–343, pl. 34, figs. 2, 4) described a coral occurring in the mid-Llandovery Brassfield Formation of Ohio as *P. conferta*. It has tabularia with diameters (outside?) of 1.0–1.5 mm and some trabecular thickening of walls, but differs from *P. thebesensis* by possessing much broader coenenchymal dissepiments and having wider spacing of tabularia in some cases.

Sokolov (1950b) described and illustrated two species from the Lower Silurian of Tunguska, Siberia, that may be conspecific with *P. thebesensis*. *Propora conferta* var. *tunicata* and *Propora cancellatiformis* both have circular, close-spaced tabularia with diameters (outside?) of about 1.0–1.4 mm, and globose coenenchymal dissepiments. Sokolov (1950b) also described *P. conferta* from the Llandovery–Wenlock (?) of the same region. It is similar to *P. thebesensis*, but has tabularia with larger diameters (outside?) of 1.6–1.7 mm and apparently broad spacing.

Propora thebesensis may also be conspecific with *Propora* cfr. *magnifica* and *Propora yabei*, both documented by Ozaki (1934) from the Ken-niho Conglomerate of northwest Korea ("Gotlandian" according to Shimizu *et al.*, 1934, pp. 59, 60, 82; possibly Llandovery). These taxa have smooth-walled, close-spaced tabularia with diameters (outside?) of about 1.3 mm (size for *P. yabei* based on photographs), and globose coenenchymal dissepiments.

Propora multispinosa Lin and Chow (1977, pp. 182, 183, fig. 22, pl. 53, figs. 1a–d), from the Ashgill of Chekiang and Kiangsi provinces in China, has crenulate, moderately thick-walled tabularia with diameters of about 1.0–1.2 mm. It differs from *P. thebesensis* by having broader coenenchymal dissepiments and, apparently, some septal spines.

Among European species, *P. thebesensis* is similar to the following: *Propora cancellata* Lindström (1899, p. 95, pl. 9, figs. 27–30), from Borkholm, Estonia (probably Ashgill, F_{II}, Porkuni Stage; Twenhofel, 1916, pp. 293, 306; Rõõmusoks, 1960, table 1); *P. conferta* as discussed and illustrated by Lindström (1899, p. 94, pl. 9, figs. 16–22) from Dalarna (Dalecarlia in Lindström), Sweden (*Leptaena* limestone or brachiopod schists of Lindström: probably Ashgill; Jaanusson, 1963, table 2); and *P. affinis* as described and illustrated by Kiaer (1930, p. 67, pl. 4, fig. 6, pl. 5, figs. 4, 5) from Stord, Norway (possibly Upper Ordovician). *Propora cancellata* is similar to *P. thebesensis* in its smooth-walled, moderately close-spaced tabularia with diameters of about 1 mm, but has very long, platy exothecal projections that make parts of its coenenchyme look similar to that of *Plasmopora*. Lindström's *P. conferta* and Kiaer's *P. affinis* resemble *P. thebesensis* by having smooth-walled or slightly crenulate tabularia, the former with diameters of about 1.0–1.5 mm and the latter with diameters of 1.1–1.3 mm (outside?), but have wider tabularium spacing and broad, gently curved coenenchymal dissepiments.

Propora thebesensis and its probable relatives *P. affinis* and *P. conferta* bear some strong similarities to two important younger species, *Propora exigua* (Billings) and *Propora tubulata* (Lonsdale). *Propora exigua*, which was recently described and discussed by Scrutton and McCurry (1987, p. 61, figs. 2d, 2e) and by Young and Noble (1990b, pp. 191, 193, table 2, figs. 2, 5.6–5.11, 6.1), is characteristic of the Telychian in northern Europe and eastern North America. It differs from members of the *thebesensis* group by having significantly smaller tabularia (diameters of 0.4–0.9 mm) that are much more broadly spaced, but is otherwise very similar to these species and is almost certainly descended from one of them. *Propora tubulata* is widespread in Europe and eastern North America, from the lower Lower Silurian (Upper Llandovery) to the lower Upper Silurian (Ludlow) (see Young and Noble, 1990b, pp. 188, 190, 191, table 1, figs. 2, 5.1–5.6; Scrutton, 1993). It is distinguished from *P. thebesensis* by its thick, commonly abundant septal spines. Its characters also suggest descent from a member of the *thebesensis* group.

Occurrences.—Uppermost Ordovician (Gamachian): lower Keel Formation, south-central Oklahoma; Leemon Formation, southern Illinois. Uppermost Ordovician (Gamachian) to lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): Cyrene Formation, northeastern Missouri. Uppermost Ordovician (?; Gamachian?) to lowermost Silurian (Lower Llandovery, lower Rhuddanian): Wilhelmi Formation, northeastern Illinois. Uppermost Ordovician (?; Gamachian?) to lower Lower Silurian (Lower Llandovery, upper Rhuddanian): lower and upper Mosalem Formation, northwestern Illinois. Lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): Kissenger Limestone Member, Bryant Knob Formation, northeastern Missouri.

Uppermost Ordovician (Gamachian) to lower Lower Silurian (Lower Llandovery, Rhuddanian): Ellis Bay and Becscie formations, Anticosti Island, Québec. Possibly in Upper Ordovician (Ashgill, pre-Hirnantian): Grande Coupe beds, Matapédia Group, near Percé, Québec. Possibly in lower Lower Silurian (Lower Llandovery, Rhuddanian): Manitoulin Formation, Manitoulin Island and Owen Sound area, Ontario.

Lectotype.—Designated here: USNM 84863b (Foerste, 1909, pl. 4, fig. 69b; Pl. 3, figs. 1, 2), collected by A. F. Foerste (labelled "*Lyellia thebesensis*, Brassfield [Formation], 1 mi. N. of Thebes"), Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois.

Paralectotype.—Designated here: USNM 84863a (Foerste, 1909, pl. 4, fig. 69a; Pl. 3, fig. 3), collected by A. F. Foerste (labelled "*Lyellia thebesensis*, Brassfield [Formation], 1 mi. N. of Thebes"), Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois.

Other material described above.—87 specimens: USNM 459087, 485700, site 23i, USNM 485701–485703, site 23ii, USNM 458777, 459075, 485704, 485705, 485706a, 485706b, site 23iii, interval 23-2 (*Brevilamnulella* beds), USNM 485707–485709, site 23i, interval 23-2a, Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; UI X-908, C-1437d, collected by T. E. Savage (labelled "*Lyellia thebesensis*, Edgewood [Formation], near Thebes"), UI C-3085a, collected by T. E. Savage (labelled "*Lyellia thebesensis*, Edgewood [Formation], Thebes"), USNM 459083, 485710–485718, interval 31-1, USNM 485719–485721, interval 31-1b, Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois; UI C-1358, collected by T. E. Savage (labelled "*Favosites* cf. *venustus* with *Heliolites*, Sexton Creek [Limestone], Alexander Co.," but lithology and coral are characteristic of Leemon Formation at Section 31), probably Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois; UI C-880, C-886a, collected by T. E. Savage (labelled "*Lyellia thebesensis*, Edgewood [Formation], near Gale"), Leemon Formation, Gale Section, Alexander County, Illinois; USNM 485722, 485723a, 485723b, 485724, interval 18-3, USNM 459084, interval 18-4, Kissenger Limestone Member, Bryant Knob Formation, Section 18 (Kissenger), Pike County, Missouri; UI C-1462a, C-1462c, collected by T. E. Savage (labelled "*Lyellia thebesensis*, Edgewood [Formation], 3 mi. S. Clarksville"), UI C-1466b, collected by T. E. Savage (labelled "*Favosites subelongus*, Edgewood Ls., 3 mi. S. Clarksville"), Bryant Knob Formation, 5 km south of Clarksville, Pike County, Missouri; USNM 459077, interval 16-1, USNM 459076, 485725, 485726, interval 16-2, Kissenger Limestone Member, Bryant Knob Formation, Section 16 (Clinton Spring), Pike County, Missouri; USNM 485727a, 485728–485738, interval 15-1, Kissenger Limestone Member, Bryant Knob Formation, Section 15 (Calumet), Pike County, Missouri; USNM 485739–485757, interval 14-1, Kissenger Limestone Member, Bryant Knob Formation, Section 14 (Higginbotham Farm), Pike County, Missouri; UI C-865a, C-865c, C-865d, C-865f, collected by T. E. Savage (labelled "*Lyellia thebesensis*, Edgewood [Formation], Edgewood"), Cyrene Formation, near Edgewood, Pike County, Missouri; UI C-1590, collected by T. E. Savage (labelled "*Lyellia thebesensis*, 1 mi. below Channahon ls. otc."), Wilhelmi Formation, 3.2 km south of Channahon, Will County, Illinois; USNM

485758, interval 32-1z, USNM 485759–485763, interval 32-1c, Mosalem Formation, Section 32 (Thomson East), Carroll County, Illinois.

Propora savagei, new species
Plate 5, figures 1–10; Plate 6, figures 1–4

Derivation of name.—The species name honors T. E. Savage, who did important early work on the uppermost Ordovician and lowermost Silurian in the east-central United States, and who collected many of the specimens described here.

Diagnosis.—*Propora* with crenulate tabularia having pronounced exothecal projections; adult tabularium diameter usually 1.0–2.0 mm, tabularium area about 30–50% of corallite area. Septa have thickened bases and spinose adaxial extensions; other distinct trabeculae commonly occur between septal trabeculae in walls. Coenenchymal dissepiments broad.

Description of coralla.—Coralla are most commonly of high bulbous growth form, rarely low bulbous or columnar (Table 14). Most are very small; measured specimens are 10–19 mm wide and 11–19 mm high.

In transverse section, tabularia are usually crenulate (Pl. 5, figs. 5, 9, Pl. 6, fig. 1), rarely smooth-walled (Pl. 5, fig. 8); pronounced exothecal projections are common (Pl. 5, figs. 7, 9). Adult tabularia commonly have diameters of 1.0–2.0 mm (Table 15). Tabularia are closely spaced, tabularium area is usually 30–50% of corallite area (Table 15); spacing is rarely so close that tabularia are compressed into subpolygonal shapes. In longitudinal section, tabularia are generally straight or gently curved, more strongly curved in lateral parts of each corallum (Pl. 6, fig. 2).

Corallite walls are thick, commonly 0.10–0.20 mm (Table 15). Walls are slightly thickened at septa in some specimens. Trabeculae from which pointed or ragged exothecal projections are developed occur at or between septa (Pl. 5, fig. 7, Pl. 6, fig. 3). Septa number 12, with basal ridges having variably developed, upwardly directed spines. Spines may be thick and square-ended (Pl. 5, fig. 5), slender (Pl. 6, figs. 3, 4), or slightly ragged (Pl. 5, fig. 3). Septal length is usually 20–30% of tabularium radius (Table 15). In a few coralla, septal spines are rare (Pl. 5, figs. 7, 9, 10).

Tabulae are of medium thickness, flat, slightly to strongly concave (Pl. 5, fig. 2) or slightly convex. They are usually complete (Pl. 5, figs. 4, 10), but are rarely incomplete (Pl. 6, fig. 2). Tabulae are usually wide-spaced, averaging about seven in 5 mm (Table 15); dense spacing is rare (Pl. 5, fig. 2). Tabular spacing shows cyclomorphic variation in some cases (Pl. 6, fig. 2). A single tabula may have variable thickness between axial and lateral parts; spines rarely project from the upper surfaces of thickened tabulae (Pl. 5, fig. 6).

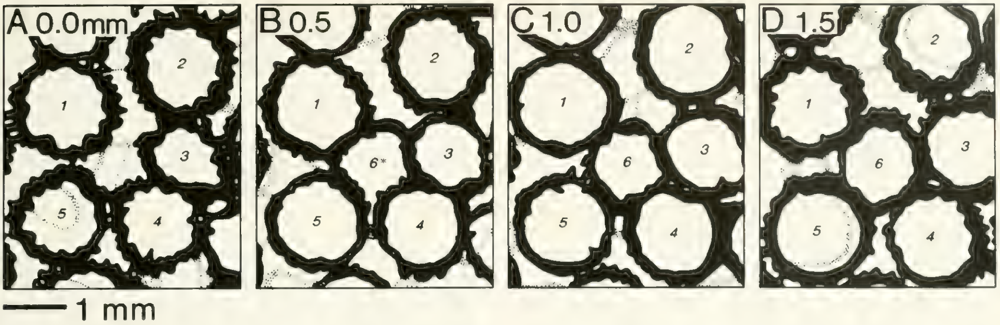
In longitudinal section, coenenchyme is usually composed of broad, flattened dissepiments (Pl. 5, figs. 4, 10), averaging about 13 in 5 mm (Table 15). Dissepiments are about twice as numerous as corallite tabulae in a unit of vertical distance (Table 15). Dissepiments are extremely broad in some coralla (Pl. 5, fig. 10), but where tabularia are closer together, dissepiments are more globose or appear as flat plates. Coenenchymal thickening is variable; dissepiments are more commonly thickened near corallite walls, but some also show a degree of cyclomorphic thickening (Pl. 6, fig. 2). Dissepiments commonly bear short, node-like structures on their upper surfaces (Pl. 5, figs. 4, 6, 10). These structures usually consist of the outer parts of exothecal wall projections, but in some coralla rare vertical rods or spines occur in the coenenchyme (Pl. 5, fig. 10). Dissepiments appear as sparsely distributed plates in transverse section.

Astogeny and corallite increase.—A single, serial-sectioned corallum (USNM 485766) is the basis for detailed observation. Other specimens are used for comparison.

The absolute base of the corallum is unknown. Close to the base, thick-walled corallites occur in a small group, with moderately close spacing. During subsequent growth, this group of axial corallites became slightly wider-spaced. There is some vertical variation in spacing and thickening of elements with height in the corallum, but these characters do not change in any consistent way in the transition from basal to subsequent growth. There is no evidence that growth patterns changed near the end of each colony's life. Corallites commonly extend through much of the height of a corallum.

Corallite increase is coenenchymal. In most examples, tabularia that are of nearly adult size were initiated on the upper surfaces of flattened coenenchymal dissepiments (Text-fig. 16A, B; Pl. 5, figs. 6, 10, Pl. 6, fig. 2). These new tabularia expanded rapidly (Text-fig. 16B–D). In transverse section, new tabularia initiated in such settings are not easily distinguished from adult tabularia. Corallite initiation between more densely spaced adult tabularia is much rarer than in *Propora thebesensis* (see *Astogeny and corallite increase* under *Propora thebesensis*, p. 49). In such cases the base of each initiate shows a gradual transition in character of horizontal elements, from coenenchymal dissepiments to tabulae. New tabularia in close-spaced settings expanded more slowly and may be subpolygonal in transverse section. Most increase was spread through the vertical growth of the corallum, but bursts of concentrated increase do occur in certain horizontal bands.

Growth of most coralla was largely vertical. Corallite



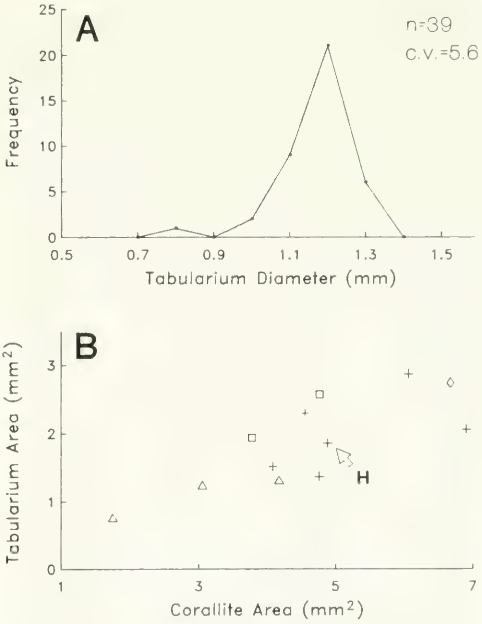
Text-figure 16.—**A–D**, Serial transverse sections illustrating corallite increase in a corallum of *Propora savagei;* USNM 485766 (paratype), Section-interval 20-6 (Short Farm) (see also Pl. 5, figs. 7–10). Corallite walls and septa are solid, tabulae and dissepiments are stippled; scale bar is shown. Heights in mm are above an arbitrary datum within a mature, axial part of the corallum; numbers in italics represent individual corallites; the asterisk beside *6* in B indicates the first appearance of that corallite.

divergence in such coralla is slight, but spacing of corallites is somewhat denser in the corallum axis than in the margins. Vertical spacing of tabulae is broader in the axis than the margins (Pl. 6, fig. 2). Cyclomorphic variation in thickening of elements is subtle, but bands appear to extend across the entire corallum.

Areas representing partial mortality of the growth surface occur in some coralla. New corallites of nearly adult size were initiated across the upper surface of a thin holotheca occurring above such an area. Corallites immediately lateral to areas of partial mortality sometimes show marked constriction followed by rejuvenation (Pl. 5, fig. 6). Regeneration is sometimes associated with a changed direction of growth indicative of reorientation during colony growth.

Microstructure.—Corallite walls are trabecular; a trabecula occurs at the base of each septum, but in most corallites other trabeculae between these give the walls their thickened appearance (Pl. 5, fig. 7). In some corallite walls, a total of 19 or 20 trabeculae can be recognized in transverse section. Exothecal projections may be developed from all trabeculae in a wall, and thus occur both at and between septa (Pl. 5, fig. 9). Tabulae are embedded in adaxial edges of wall trabeculae, while coenenchymal dissepiments are embedded deeper in the wall (Pl. 5, fig. 3).

Intraspecific variation.—Since relatively few coralla are known, many aspects of intraspecific variation cannot be analyzed in detail. The frequency distribution of tabularium size for one corallum is close to a normal distribution, but with slight negative skewness (Text-fig. 17A). Tabularium area and corallite area show a strong positive correlation (Text-fig. 17B). There seem to be distinctions among localities for these characters,



Text-figure 17.—Intraspecific variation in *Propora savagei.* **A**, Tabularium size-frequency distribution for a transverse section; USNM 485766 (paratype), Section-interval 20-6 (Short Farm). n = number of tabularia, c.v. = coefficient of variation. **B**, Relationship between mean tabularium area and mean corallite area for transverse sections; H = UI X-8722 (holotype). Symbols for Section-intervals: □ 23-3 (Lawrence Quarry); n (number of coralla) = 2; + 31-1 and 31-1b (Thebes North); n = 6; △ 20-1 and 20-6 (Short Farm); n = 3; ◇ 14-1 (Higginbotham Farm); n = 1.

but because most coralla are small, absolute measurements of size and spacing of internal features should be interpreted with some caution. In relative terms, the two coralla from the Keel oölite in Section-interval 23-3 (Lawrence Quarry) have more closely spaced tabularia than do those from other localities, such as Section-intervals 31-1 (Thebes North) and 20-6 (Short Farm).

Morphologic characters of this species generally show little or no variation between most localities; these features include tabularium diameter, form of septa, appearance of coenenchymal dissepiments and tabulae, and patterns of thickening of elements. The only important differences are those between the three specimens from Section 20 (Short Farm) and coralla from all other localities (see *Discussion*, below).

Discussion.—These coralla are assigned to a new species, *Propora savagei*. This species has close affinities with *Propora thebesensis*, but is recognized as distinct on the basis of its usually larger and more widely spaced tabularia (Text-fig. 15), thicker walls, broad and flattened coenenchymal dissepiments, and common occurrence of thickened wall trabeculae between septa. It probably evolved from *P. thebesensis*, or from a closely related older coral such as *Propora conferta* as described and illustrated by Bolton (1980, p. 20, pl. 2.4, figs. 1–3, 9, 10, pl. 2.5, fig. 7) from the Grande Coupe beds of the Matapédia Group near Percé, Québec (Upper Ordovician, Ashgill, pre-Hirnantian; Lespérance *et al.*, 1987, fig. 4) (see *Discussion* under *P. thebesensis*, p. 54).

A few coralla from Section 20 (Short Farm) are especially similar to *P. thebesensis* in several characters, including tabularium diameter, form of coenenchyme, and thickening of corallite walls. These are among the oldest specimens of *P. savagei*, and may have belonged to a transitional population. *Propora savagei* occurs only in the east-central United States and is not known from north of northeastern Missouri. It is generally found in strata that were probably deposited under high-energy conditions, such as Section-intervals 23-3 (Lawrence Quarry), 31-1 (Thebes North), and 14-1 (Higginbotham Farm). This species may thus represent a specialized local variant belonging to the *thebesensis* group. *Propora savagei* was referred to as *Propora* n. sp. aff. *P. thebesensis* by Elias and Young (1992, fig. 2, tables 1, 2).

Propora savagei is somewhat similar to *Propora speciosa*, which is also found in uppermost Ordovician to lowermost Silurian rocks of the east-central United States. *Propora speciosa*, however, has much larger tabularia (diameters commonly 2–3 mm), common or abundant rods in the coenenchyme, and longer, thicker, more abundant septal spines (Pl. 6, figs. 5–10, Pl. 7, figs. 1–8; see under *P. speciosa*, p. 59). *Propora* sp. aff. *P. speciosa* of Bolton (1981a, pl. 11, figs. 3, 4), from the Jupiter Formation on Anticosti Island, Québec (lower Lower Silurian, Middle–Upper Llandovery, upper Aeronian–Telychian; Barnes, 1988, fig. 2), has tabularia that are just slightly larger than those of *P. savagei*. It is differentiated from the latter by its irregular and incomplete tabulae that often have their upper surfaces covered with small spinules, and by its weaker septal thickenings and apparent lack of septal spines.

Occurrences.—Uppermost Ordovician (Gamachian): lower Keel Formation, south-central Oklahoma; Leemon Formation, southern Illinois and southeastern Missouri. Uppermost Ordovician (Gamachian) to lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): Cyrene Formation, northeastern Missouri. Lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): Kissenger Limestone Member, Bryant Knob Formation, northeastern Missouri.

Holotype.—UI X-8722 (Pl. 5, figs. 5, 6), collected by T. E. Savage (labelled "*Lyellia thebesensis*, Edgewood [Formation], Thebes, Illinois"), Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois.

Paratypes.—Three specimens: USNM 485764 (Pl. 5, figs. 1–3), site 23ii, interval 23-3, Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; USNM 485765 (Pl. 6, figs. 1, 2), interval 20-1, USNM 485766 (Pl. 5, figs. 7–10), interval 20-6, Leemon Formation, Section 20 (Short Farm), Cape Girardeau County, Missouri.

Other material described above.—12 specimens: USNM 485767, 485768, site 23i, interval 23-3, Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; UI C-1437b, C-1437c, collected by T. E. Savage (labelled "*Lyellia thebesensis*, Edgewood [Formation], near Thebes"), USNM 485769, 485770a, 485771, 485772, interval 31-1, USNM 485773, interval 31-1b, Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois; USNM 485774, interval 20-6, Leemon Formation, Section 20 (Short Farm), Cape Girardeau County, Missouri; USNM 485775, interval 14-1, Kissenger Limestone Member, Bryant Knob Formation, Section 14 (Higginbotham Farm), Pike County, Missouri; UI C-865e, collected by T. E. Savage (labelled "*Lyellia thebesensis*, Edgewood [Formation], Edgewood"), Cyrene Formation, near Edgewood, Pike County, Missouri.

Propora speciosa (Billings, 1865)

Plate 6, figures 5–10; Plate 7, figures 1–8

Heliolites speciosus Billings, 1865, pp. 426, 427; 1866, pp. 30, 31, fig. 13.

Propora speciosa (Billings, 1865). Lindström, 1899, pp. 95, 96 [*par-*

tim], pl. 9, figs. 40–42 [*non* pl. 9, figs. 43–46, pl. 10, figs. 1–5]; Dixon, 1974, pp. 580–583, figs. 7, 8, pl. 3, figs. 1–10; Bolton, 1981a, pl. 2, fig. 5.

Propora (*Pinacopora*) *girvanensis* (Nicholson and Etheridge, 1880). Lindström, 1899, pl. 9, figs. 36–39.

Pinacopora grayi Nicholson and Etheridge, 1878. Lindström, 1899, p. 99.

Lyellia americana Milne-Edwards and Haime, 1851. Lambe, 1899, pp. 85, 86 [*partim; non* pl. 5, figs. 2, 2a].

Calvinia edgewoodensis Savage, 1913, p. 66, pl. 12, figs. 15–17; 1917, p. 116, pl. 4, figs. 15–17.

Cavella edgewoodensis (Savage, 1913). Stechow, 1922, pp. 152, 153.

Lyellia speciosa (Billings, 1865). Twenhofel, 1928, p. 135.

[*cf.*] *Propora magna* Sokolov, 1955, pl. 78, figs. 1, 2; 1962, pl. 5, figs. 2a, 2b.

[?] *Propora speciosa* (Billings, 1865). Bolton, 1980, p. 20, pl. 2.5, figs. 1, 3, 6; Bondarenko and Minzhin, 1981, pp. 7–12, figs. 1–3, pl. 1, figs. 1–4, pl. 2, figs. 1–4.

Diagnosis.—*Propora* with crenulate tabularia; adult tabularium diameters about 2–3 mm, tabularium areas about 25–50% of corallite areas. Thickened septal bases commonly bear thick spines; distinct trabeculae commonly occur between septal trabeculae in corallite walls. Thick trabecular rods pass vertically through small, globose coenenchymal dissepiments.

Description of coralla.—Growth form can be determined for only two specimens. One (UI X-850) is of high bulbous form, 76 mm wide and 53 mm high; the other (UI C-1438) is high domical, 82 mm wide and 48 mm high.

In transverse section, tabularia are circular or subcircular, and markedly crenulate in outline (Pl. 7, figs. 1, 8); short exothecal projections are rare to common (Pl. 7, figs. 1, 3, 7). Adult tabularia commonly have diameters of 2.0–2.8 mm (Table 15). Tabularia are moderately closely spaced, but walls of adjacent corallites are never in contact. Tabularium area is usually about 30% of corallite area (Table 15). In longitudinal section, tabularia are straight or slightly curved.

Walls are thick, commonly 0.15–0.25 mm (Table 15), with greater thickening at septal bases. Most thickening occurs on inner edges of walls. Walls appear to be incomplete in places. Septa are often long (Pl. 6, fig. 8, Pl. 7, figs. 1, 3), about 55–75% of tabularium radius (Table 15). Thickened septal bases bear thick, common to abundant spines that are angled upwards (Pl. 6, figs. 7, 10). Thickening of walls and development of septa may both vary cyclomorphically.

Tabulae are thin, complete or incomplete, and flat, wavy, or concave (Pl. 6, fig. 10, Pl. 7, fig. 2). They are variably spaced, averaging about five in 5 mm (Table 15). Spacing of tabulae can show distinct cyclomorphic variation, but thickness does not seem to vary significantly (Pl. 7, fig. 2). Pairs of densely spaced and widely spaced bands in one measured corallum average 7.3 mm in thickness. Incomplete tabulae are more common in bands where spacing is dense.

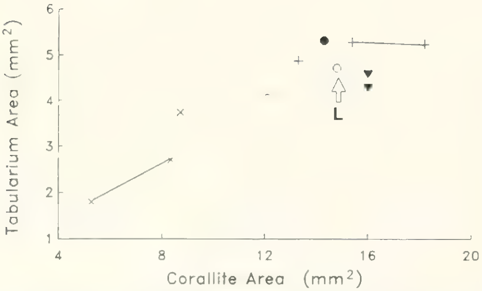
In longitudinal section, coenenchyme is composed of small, globose, moderately regular dissepiments. Dissepiments are wide-spaced, averaging about nine in 5 mm; ratio of corallite tabulae to dissepiments per unit of vertical distance is about 0.6 (Table 15). Spacing and thickening of dissepiments show some cyclomorphic variation (Pl. 7, fig. 2). Vertical skeletal elements are common to abundant in coenenchyme; these most commonly take the form of thick trabecular rods 0.125–0.225 mm in diameter and several mm long. These rods are oriented parallel to wall trabeculae and pass through coenenchymal dissepiments (Pl. 6, fig. 10, Pl. 7, fig. 5). Vertical elements may also occur as small tubercles on the upper surfaces of dissepiments (Pl. 7, fig. 2). In transverse section, coenenchymal dissepiments are thin and sparsely distributed; rods are regularly distributed between corallite walls (Pl. 7, figs. 1, 8).

Astogeny and corallite increase.—The basal parts of coralla are unknown. Preservation does not permit comparison of axial and marginal parts.

Corallite increase is coenenchymal. Tabularia that are often strongly crenulate and of nearly adult size were initiated on the upper surfaces of coenenchymal dissepiments (Pl. 6, fig. 10). In some cases, coenenchymal rods occurring below the corallite are extended upwards into wall trabeculae (Pl. 6, fig. 10, Pl. 7, fig. 2).

A sediment inclusion representing partial colony mortality occurs in a single corallum (Pl. 6, fig. 9). Above the inclusion, new corallites of nearly adult size were initiated across the upper surface of a thin holotheca. Coenenchymal trabeculae also extend upward from the holotheca, occurring in a coenenchyme of normal appearance.

Microstructure.—Corallite walls are trabecular; a trabecula occurs at the base of each septum, and other trabeculae occur in the wall between the septa. Usually one or two trabeculae occur between each pair of septal trabeculae (Pl. 7, figs. 3, 4), but three trabeculae are occasionally observed. Walls sometimes appear incomplete, with spaces occurring laterally between trabeculae (Pl. 7, fig. 7), but this may be a preservational feature. Exothecal projections may be developed from trabeculae located at any position in the wall. The trabecular rods in the coenenchyme are subcircular or irregular in transverse section and are almost radially symmetrical (Pl. 6, fig. 8, Pl. 7, figs. 3, 8); they are very similar in appearance to wall trabeculae. In some places the two types merge vertically or laterally, suggesting that they are homologous structures (Pl. 6, fig. 10, Pl. 7, fig. 2). Thick septal spines extend adaxially from the



Text-figure 18.—Relationship between mean tabularium area and mean corallite area in *Propora speciosa* (and probable synonyms) from several regions. Each data point represents a single transverse thin section, except as otherwise stated; solid lines connect sections from different parts of a single corallum. Symbols for Section-interval and other occurrences: + 31-1 (Thebes North); n (number of coralla) = 2; ▼ Gale Section; n = 2; ○ Ellis Bay Formation, Anticosti Island, Québec; GSC 2240a (L = lectotype), 2240 (paralectotype); n = 2; ● Ellis Bay Formation, Anticosti Island, Québec; mean for 46 coralla (data from Dixon, 1974, table 4); × Grande Coupe beds, Matapédia Group, near Percé, Québec; n = 2.

wall trabeculae; they are fibrous and are continuous with the fibers of the trabeculae. In some cases septal tips are downcurved (Pl. 6, fig. 10). Tabulae are embedded in the innermost edges of wall trabeculae and in some cases are suspended from septal spines (Pl. 6, fig. 10). Coenenchymal dissepiments are embedded somewhat deeper in the wall trabeculae (Pl. 6, fig. 7). Microstructure of tabulae and dissepiments can not be determined.

Intraspecific variation.—The five specimens from the east-central United States are remarkably consistent with one another in characters that are analyzed numerically. These include tabularium and corallite areas, wall thickness, septal development, and spacing of tabulae and dissepiments. On a graph of tabularium area *versus* corallite area (Text-fig. 18), the difference in corallite area between sections from a single corallum (UI C-889a) is almost as great as the overall variation for all plotted specimens from the east-central United States. Obvious differences in appearance between the studied specimens are largely due to variation in the degree and pattern of thickening of skeletal elements (*e.g.*, compare Pl. 6, fig. 10, with Pl. 7, fig. 2; see *Propora speciosa*, p. 38).

Discussion.—*Propora speciosa* was first described by Billings (1865, 1866) from member 2 of the lower part of the Ellis Bay Formation on Anticosti Island, Québec (uppermost Ordovician, Gamachian; Barnes, 1988, fig. 2) (see Dixon, 1974, p. 582). We examined Billings' two syntypes of *Heliolites speciosus* and designate them as lectotype (GSC 2240a) and paralectotype (GSC 2240). Both coralla have crenulate tabularia and their coenenchymes possess trabecular rods; the lectotype and paralectotype, respectively, have mean tabularium diameters of 2.45 mm and 2.27 mm, and tabularium areas averaging 32% and 33% of corallite areas (measurements made on external surfaces). These characters are very similar to those for the specimens from the east-central United States (see Table 15; Text-fig. 18); the slightly smaller size of tabularia in GSC 2240 may be attributed to the small size of this corallum (about 27 mm wide, 50 mm high).

Specimens of *P. speciosa* from member 7 at the top of the Ellis Bay Formation on Anticosti Island (Gamachian to possibly lowermost Silurian, Lower Llandovery, lowermost Rhuddanian; Melchin *et al.*, 1991, p. 1861) were described and discussed in detail by Dixon (1974; unit referred to as member 6 therein). They have crenulate tabularia with a mean diameter of 2.6 mm, tabularium areas averaging 37% of corallite areas, spinose septa, and trabecular rods in their coenenchymes. These features are very similar to those for coralla from the east-central United States (see Table 15; Text-fig. 18); the only discernable difference is that the specimens from Anticosti tend to have a lesser degree of thickening of skeletal elements. We agree with Dixon (1974, p. 583) on the synonymization of other Anticosti occurrences of this species. These include the material from Junction Cliff (lower Ellis Bay Formation) illustrated by Lindström (1899) as *P. speciosa* and as *Propora* (*Pinacopora*) *girvanensis* (referred to by Lindström in his text as *Pinacopora grayi*), and other specimens from Junction Cliff listed by Lambe (1899) in his description of *Lyellia americana*. Twenhofel (1928) recognized *Lyellia speciosa* at several levels in the Ellis Bay Formation.

More recently, a corallum of *P. speciosa* from member 7 of the Ellis Bay Formation was illustrated by Bolton (1981a; member 6 interbiohermal therein). This specimen has tabularia with diameters of about 2.5 mm, globose coenenchymal dissepiments, and sparse coenenchymal trabeculae. Bolton's (1981a, pl. 11, figs. 3, 4) *Propora* sp. aff. *P. speciosa* from the Jupiter Formation (Middle–Upper Llandovery, upper Aeronian–Telychian; Barnes, 1988, fig. 2) is distinguished from *P. speciosa* by having irregular or incomplete tabulae that bear small spinules on their upper surfaces, and by lacking septal spines and possessing slightly smaller tabularia.

The specimens described and illustrated here from the east-central United States include the type specimen (UI X-850) of *Calvinia edgewoodensis* (= *Cavella edgewoodensis* according to Stechow, 1922), which is the type species of *Calvinia* (= *Cavella*). Savage's (1913) recognition of *Calvinia* as a new genus was based on the misinterpretation of coenenchymal trabeculae as cylindrical tubules. Of all the material from the east-central United States, the type specimen of *C. edgewoodensis* is the most similar to *P. speciosa* from Anticosti Island (compare Pl. 7, figs. 1–4, with Dixon, 1974, figs. 7b, 8). The corallum of *P. speciosa* from Section-interval 32-1c (Thomson East) is geographically separated from, and is younger than, the four specimens from southern Illinois. Nevertheless, it is similar to them and has numerical characters that are mostly close to the species means (biometric data for USNM 485776: TaD = 2.60 mm, WT = 0.213 mm, LS = 60%; compare with Table 15). Among the other corals from the east-central United States, *P. speciosa* is most similar to *P. savagei* (see *Discussion* under *P. savagei,* p. 58).

Corals from the Grande Coupe beds of the Matapédia Group near Percé, Québec (Upper Ordovician, Ashgill, pre-Hirnantian; Lespérance *et al.,* 1987, fig. 4), were described and illustrated as *P. speciosa* by Bolton (1980; White Head Formation therein). We examined the following specimens: GSC 53531 (Bolton, 1980, pl. 2.5, figs. 1, 6), collected by G. W. Sinclair in 1956, Grande Coupe, Québec; GSC 53532 (Bolton, 1980, pl. 2.5, fig. 3), collected by P. J. Lespérance in 1962, Petite Coupe, Québec. These coralla have crenulate tabularia, spinose septa, and short trabecular rods in their coenenchymes. They differ from those in the Ellis Bay Formation of Anticosti Island by having smaller tabularium diameters of about 1.8–2.2 mm and broad coenenchymal dissepiments, and one (GSC 53532) has tabulae that bear spines on their upper surfaces. For these reasons, they are questionably synonymized with *P. speciosa* here.

A species described by Bondarenko and Minzhin (1981) as *P. speciosa* from the Ashgill Tsagan-Del beds of Mongolia may be conspecific with the North American *P. speciosa.* The Mongolian specimens have tabularia with crenulate outlines and coenenchymes with trabecular rods, but are distinguished by having somewhat smaller tabularium diameters of about 1.3–2.2 mm, by the common occurrence of long, thick, vertically oriented spines on the upper surfaces of tabulae, and by their generally broader coenenchymal dissepiments. Bondarenko and Minzhin (1981, pp. 11, 12) noted that phyletic changes in the Mongolian material include an increase in tabularium diameter, disappearance of the spines on tabulae, and an increase in the length of coenenchymal rods. This pattern is reflected in North America by the differences between the specimens from the Grande Coupe beds and those from the Ellis Bay Formation and the east-central United States.

Proporids that are similar to *P. speciosa* also occur in some parts of Baltoscandia. A specimen from the Porkuni Stage of Estonia (Ashgill, Hirnantian; Kaljo *et al.,* 1988, p. 90), illustrated and briefly described as *Propora magna* by Sokolov (1955, 1962), may be conspecific with *P. speciosa.* It has crenulate tabularia with diameters (outside?) of about 3 mm, but has thinner walls than those of *P. speciosa* and has only small trabecular tubercles, rather than rods, in its coenenchyme.

Lindström (1899, pl. 9, figs. 45, 46, pl. 10, figs. 1–5) illustrated specimens identified as *P. speciosa* from Borenshult, Östergotland (Ostrogothia in Lindström), Sweden (probably of Ordovician age), and from the Slite Beds of Gotland, Sweden (upper Lower Silurian, mid-Wenlock). These are similar to the North American *P. speciosa* in having trabecular rods in their coenenchymes, but we do not consider them to be synonymous. The Östergotland specimens have smaller tabularia with diameters of about 1.5 mm and possess broad coenenchymal dissepiments, and the material from Gotland has smaller and more broadly spaced tabularia with diameters of about 1.7 mm; both appear to lack septal spines.

Propora bacillifera Lindström (1899, p. 97, pl. 10, figs. 8–21) was erected for material from the following locations: Treberga, öland, Sweden (Upper Ordovician; Jaanusson and Mutvei, 1982, p. 9); Dalarna (Dalecarlia in Lindström), Sweden (Ordovician or Silurian); Kõrgessaare, Island of Hiiuama (Hohenholm in Dagö in Lindström), and Piersal, Estonia (both Upper Ordovician, F_I, Nabala, Vormsi, or Pirgu Stage; Twenhofel, 1916, pp. 293, 294; Rõõmusoks, 1960, table 1); Borkholm, Estonia (Ashgill, F_{II}, Porkuni Stage; Twenhofel, 1916, pp. 293, 306; Rõõmusoks, 1960, table 1); Island of Herøy (?; Herö in Lindström), Norway; and Gotland, Sweden (Röda Lagret?; Upper Llandovery, Telychian). Like *P. speciosa,* this species has trabecular rods in its coenenchyme, but its tabularia have diameters of about 3 mm and are more broadly spaced, and it possesses very long and thick septal spines.

Propora bacillifera has also been described and illustrated by Kiaer (1930, p. 68, pl. 5, figs. 2, 3) from the Upper Ordovician of Stord, Norway. Kiaer's material has broadly spaced tabularia with diameters of about 1.8–1.9 mm, and has weakly developed coenenchymal trabeculae and septal spines. It is more similar to *P. speciosa* than to Lindström's *P. bacillifera,* but is probably not conspecific with either species.

Plasmopora conferta (Milne-Edwards and Haime) was identified from the Bønsnes Formation of Ringerike, Norway (Ashgill, Rawtheyan; Owen *et al.,* 1990, p. 37), by Kiaer (1899, pp. 27, 28, pl. 4, figs. 3, 4; Gastropodenkalk, Etage 5a therein). It has spinose septa, coenenchymal trabeculae, and tabularium diameters of about 1.8–3.2 mm, but has much broader coenenchymal dissepiments than those of *P. speciosa.*

Occurrences.—Uppermost Ordovician (Gamachian): Leemon Formation, southern Illinois. Lower Lower Silurian (Lower Llandovery, upper Rhuddanian): upper Mosalem Formation, northwestern Illinois.

Uppermost Ordovician (Gamachian) to lowermost Silurian (?; Lower Llandovery?, lowermost Rhuddanian?): Ellis Bay Formation, Anticosti Island, Québec. Possibly in Upper Ordovician (Ashgill, pre-Hirnantian): Grande Coupe beds, Matapédia Group, near Percé, Québec. Possibly in Upper Ordovician (Ashgill): Tsagan-Del beds, Mongolia.

Lectotype.—Designated here: GSC 2240a (Pl. 6, fig. 5), collected by T. C. Weston in 1865, Ellis Bay Formation, White Cliff, Ellis Bay, Anticosti Island, Québec.

Paralectotype.—Designated here: GSC 2240, collected by T. C. Weston in 1865, Ellis Bay Formation, White Cliff, Ellis Bay, Anticosti Island, Québec.

Other material described above.—Five specimens: UI C-889a, collected by T. E. Savage (labelled "*Plasmopora thebesensis,* Edgewood [Formation], Thebes"), UI C-1438, collected by T. E. Savage (labelled "*Calvinia edgewoodensis,* Edgewood [Formation], near Thebes"), Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois; UI X-850 (type specimen of *C. edgewoodensis*), C-1440, collected by T. E. Savage (labelled "*Calvinia edgewoodensis,* Edgewood [Formation], near Gale"), Leemon Formation, Gale Section, Alexander County, Illinois; USNM 485776, interval 32-1c, Mosalem Formation, Section 32 (Thomson East), Carroll County, Illinois.

Propora species aff. **P. affinis** (Billings, 1865)
Plate 7, figures 9, 10

[*aff.*] *Heliolites affinis* Billings, 1865, pp. 427, 428; 1866, pp. 5, 6.
[*aff.*] *Propora conferta* Milne-Edwards and Haime, 1851. Bolton, 1981a, pl. 9, fig. 1, pl. 11, figs. 1, 2.

Description.—The single corallum of this species is broken. It is of low domical growth form, 58 mm wide and 21 mm high.

In transverse section, tabularia are usually smooth-walled or have slightly wavy walls, but are crenulate where skeletal elements are thickened. Adult tabularia commonly have diameters of 1.0–1.3 mm (Table 15). Tabularia are moderately close-spaced, with tabularium areas averaging 38% of corallite areas (Table 15). In longitudinal section, tabularia are elongate, and straight or gently curved (Pl. 7, fig. 10).

Corallite walls are thin, but exhibit cyclomorphic thickening; thickness varies from 0.025–0.100 mm (Table 15). Septa are absent or are represented by 12 thickened trabecular ridges in cyclomorphically dense parts of the corallum. Septal length is 0–25% of tabularium radius (Table 15). Exothecal projections from septa are rare and small. Tabulae are thin, mostly complete, and flat to strongly concave. Spacing varies cyclomorphically (Pl. 7, fig. 10), averaging about 10 tabulae in 5 mm (Table 15). Tabulae are more densely spaced in bands having thickened skeletal elements; pairs of dense and less dense bands average 4.0 mm in thickness.

In longitudinal section, coenenchyme is composed of globose to moderately broad domed dissepiments. Dissepiments are usually thin and widely spaced; they are more closely spaced in cyclomorphically dense bands. Dissepiments average 13.5 in 5 mm; ratio of corallite tabulae to dissepiments per unit of vertical distance is about 0.8 (Table 15). In transverse section, dissepiments are sparsely distributed.

Corallite increase is coenenchymal. New tabularia were initiated on the upper surfaces of coenenchymal dissepiments.

Discussion.—This corallum has close affinities with members of the group that includes *Propora affinis, Propora conferta,* and *Propora thebesensis.* However, because there is only one poorly preserved specimen, it is not considered possible to make a definite specific assignment. The name *Propora* sp. aff. *P. affinis* is used for this specimen because of its similarity in numerical characters to Billings' syntype of *P. affinis* (GSC 2340, 2340a; see *Discussion* under *P. thebesensis,* p. 53; Text-fig. 15) from the Gun River Formation (Middle Llandovery, lower Aeronian; Barnes, 1988, fig. 2) on Anticosti Island, Québec. It is also closely similar to the specimens illustrated by Bolton (1981a, pl. 9, fig. 1, pl. 11, figs. 1, 2) as *P. conferta* from the Gun River Formation and the Jupiter Formation (Middle–Upper Llandovery, upper Aeronian–Telychian; Barnes, 1988, fig. 2) on Anticosti. Bolton's specimens are distinguished from *Propora* sp. aff. *P. affinis* by their more globose coenenchymal dissepiments, and his corallum from the Gun River Formation may have slightly larger tabularia.

Propora sp. aff. *P. affinis* is distinguished from the older *P. thebesensis,* which also occurs in the east-central United States, by its larger and wider coenenchymal dissepiments, more broadly spaced tabularia (Text-fig. 15), and greatly reduced exothecal projections. A more thorough comparison of members of the *thebesensis* group is given elsewhere (see *Discussion* under *P. thebesensis,* pp. 53–55).

Occurrence.—Lower Lower Silurian (Lower Llandovery, upper Rhuddanian, or possibly Middle Llandovery, lowermost Aeronian): Elwood Formation, northeastern Illinois.

Material described above.—One specimen: USNM 485777, interval 29-4, Elwood Formation, Section 29 (Sears Pit), De Kalb County, Illinois.

Propora species A
Plate 8, figures 1, 2

Description.—The single corallum of this species is broken. It is probably of low domical growth form, more than 75 mm wide and more than 33 mm high.

In transverse section, tabularia have irregular crenulate outlines (Pl. 8, fig. 1); adult diameters are commonly 2–3 mm (Table 15). Tabularia are wide-spaced, with tabularium areas averaging 20% of corallite areas (Table 15). In longitudinal section, tabularia are almost straight or of irregular shape (Pl. 8, fig. 2).

Corallite walls are moderately thick, ranging from 0.125–0.175 mm (Table 15). Walls are composed of trabecular septal bases, with additional trabeculae irregularly distributed between them. Walls are complete where thickened, but are sometimes incomplete where unthickened; incomplete walls are composed of the lateral edges of coenenchymal dissepiments (Pl. 8, fig. 2). Septa have variably developed trabecular bases with abundant, moderately thick, straight or curved spinose extensions. Septal spines are more abundant in zones of septal thickening; they may project through tabulae and become interspersed with tabular spines (Pl. 8, fig. 2). Length of septa is about three-quarters of tabularium radius (Table 15). Exothecal projections from septa are present in some cases.

Tabulae are closely but variably spaced, averaging about 13 in 5 mm (Table 15). They are flat, convex, concave, or wavy, and incomplete or dissepimentate in some zones (Pl. 8, fig. 2). Abundant short, thick trabecular spines project from the upper surfaces of tabulae (Pl. 8, fig. 2).

In longitudinal section, coenenchyme consists of variable, low-domed to globose dissepiments; in some cases these are very broad. They commonly bear short, thick spines (diameter 0.05–0.15 mm) on their upper surfaces. Dissepiments are moderately closely spaced, about 11 in 5 mm (Table 15). They are more broadly spaced than corallite tabulae; ratio of tabulae to dissepiments per unit of vertical distance is 1.25 (Table 15). Although spacing of both tabulae and dissepiments is variable, cyclicity is poorly developed. In transverse section, coenenchyme appears as irregular curved plates interspersed with the small trabecular spines (Pl. 8, fig. 1).

Discussion.—This corallum is different from most members of *Propora* in having spines developed on its septa, tabulae, and coenenchymal dissepiments. It is clearly similar to the somewhat younger *Propora glabra* Owen (1844). The latter species was described and illustrated by Milne-Edwards and Haime (1851, pp. 226, 227, pl. 12, figs. 2, 2a–c) from the "Magnesian Limestone" of Iowa (Hopkinton Dolomite?: lower Lower Silurian, Middle–Upper Llandovery, Aeronian–Telychian; Witzke, 1992, fig. 18), and by Stumm (1965, pp. 57, 58, pl. 56, figs. 7–9) from the Manistique Dolomite of Michigan and Ontario (Upper Llandovery; Winder and Sanford, 1972, fig. 2), Hopkinton Dolomite of Iowa, and Louisville Limestone of Indiana and Kentucky (upper Lower Silurian, Upper Wenlock; Berry and Boucot, 1970, p. 180). *Propora glabra* has crenulate tabularia with diameters of about 2.0–2.5 mm, incomplete tabulae, and spines on both tabulae and coenenchymal dissepiments, but it seems to have longer and thicker septa than does the corallum described above. The *P. glabra* illustrated by Bolton (1981a, pl. 13, fig. 7), from the Chicotte Formation of Anticosti Island, Québec (Upper Llandovery, Telychian; Barnes, 1988, fig. 2), is quite different, having more widely spaced tabularia with diameters less than 2 mm and tabulae that appear to lack spines.

This corallum is identified as *Propora* sp. A. It is not assigned to a new species because only one incomplete specimen is known.

Occurrence.—Lower Lower Silurian (Lower? Llandovery, upper Rhuddanian?): Sexton Creek Limestone, southern Illinois.

Material described above.—One specimen: UI C-1403, collected by T. E. Savage (labelled "*Lyellia americana,* Sexton Creek [Limestone], Thebes"), Sexton Creek Limestone, near Thebes, Alexander County, Illinois.

Family **PLASMOPORIDAE** Sardeson, 1896

Genus **PLASMOPORA**
Milne-Edwards and Haime, 1849

Plasmopora Milne-Edwards and Haime, 1849, p. 262.
Laminoplasma Bondarenko, 1963, p. 49.
Eolaminoplasma Bondarenko, 1963, p. 50.

Type species.—By monotypy: *Porites petalliformis* Lonsdale (1839, p. 687, pl. 16, figs. 4, 4a); Wenlock Shale (upper Lower Silurian, Wenlock), Walsall, U.K.

Diagnosis.—"Plasmoporidae with corallites of smooth or crenulate outline; each corallite surrounded by a complete aureole of tubules; coenenchyme between aureoles of irregular tubules in transverse section; dissepimentate in vertical section with spines, rods, or vertical plates irregularly outlining tubules; tabulae mostly complete" (Young and Noble, 1990b, p. 194).

Table 16.—Biometric data for one corallum of *Plasmopora* sp. cf. *P. logani* (UI C-865b) from the east-central United States. *TaD* = tabularium diameter, *TaA* = tabularium area, *CoA* = corallite area, *TuD* = tubule diameter, *WT* = wall thickness, *LS* = length of septa, *Ta5* = number of tabulae in 5 mm, *Di5* = number of coenenchymal dissepiments in 5 mm; c.v. = coefficient of variation.

	parameters									
data	*TaD*	*TaA*	*CoA*	*TaA:CoA*	*TuD*	*WT*	*LS*	*Ta5*	*Di5*	*Ta5:Di5*
mean	1.32 mm	1.37 mm^2	4.12 mm^2	0.33	0.38 mm	0.056 mm	0	8.8	11.4	0.77
minimum	1.15 mm	—	—	—	0.20 mm	0.050 mm	—	6	9	—
maximum	1.45 mm	—	—	—	0.65 mm	0.075 mm	—	11	15	—
intracolony c.v.	6.7	—	—	—	26.3	19.6	—	20.5	20.2	—

Remarks.—The concept of *Plasmopora* given by Young and Noble (1990b, pp. 194, 195) is followed here. The specimen described below as *Plasmopora* sp. cf. *P. logani* is the oldest known North American *Plasmopora* and one of the oldest worldwide. It is similar in characters such as tabularium diameter and form of septa to *Propora thebesensis,* which also occurs in the east-central United States. This similarity suggests that *Plasmopora* sp. cf. *P. logani* descended from a proporid belonging to the *thebesensis* group. *Plasmopora* as presently defined is an extremely variable genus, and other species groups assigned to it appear to have evolved later from different ancestral taxa.

Plasmopora species
cf. **P. logani** Young and Noble, 1990b
Plate 8, figures 3, 4

[*cf.*] *Plasmopora follis* Milne-Edwards and Haime, 1851. Lambe, 1899, pp. 82, 83, pl. 2, figs. 8, 8a; Northrop, 1939, p. 148; Noble and Young, 1984, pp. 874, 875, figs. 5c, 5d, 8.

[*cf.*] *Pseudoplasmopora follis* (Milne-Edwards and Haime, 1851). Bolton, 1981b, pl. 3, figs. 5, 6, pl. 4, figs. 8, 9.

[*cf.*] *Plasmopora logani* Young and Noble, 1990b, p. 195, figs. 6.6–6.11, 7.1–7.3.

Description.—The single corallum is high bulbous and flat-based. It is 26 mm wide and 19 mm high.

In transverse section, tabularia are circular or subcircular, smooth-walled, rarely irregular in outline (Pl. 8, fig. 4). Adult tabularia have diameters of 1.15–1.45 mm (Table 16). Tabularium spacing is moderate; tabularium areas average 33% of corallite areas (Table 16). In longitudinal section, tabularia are straight or gently curved.

Corallite walls are regular and moderately thick; averaging about 0.06 mm, but are more thickened in places (Table 16). Thickening of walls may extend outward into walls of adjacent coenenchymal tubules. Septa are usually absent; weak septal ridges occur rarely (Pl. 8, fig. 4). Tabulae are complete, horizontal or slightly concave, and wide-spaced, averaging about nine in 5 mm (Table 16). Cyclicity of tabular spacing is poorly developed.

In longitudinal section, high-domed, narrow, thin coenenchymal dissepiments are vertically aligned but do not usually form definite tubules (Pl. 8, fig. 3); they are occasionally arranged into clearly defined tubules in some small areas. About 11 dissepiments in 5 mm; ratio of corallite tabulae to dissepiments per unit of vertical distance averages 0.77 (Table 16). In transverse section, coenenchyme is composed of polygonal tubules of variable size; average diameter about 0.4 mm (Table 16). Tubule walls are generally thin. Each tabularium is usually surrounded by an aureole of 12 tubules. One or two tubules, rarely three or four, occur between pairs of adjacent tabularia (Pl. 8, fig. 4).

Corallite increase is coenenchymal. The base of each new tabularium was initiated across the tops of several laterally equivalent coenenchymal dissepiments.

Discussion.—This corallum is remarkably similar to the younger *Plasmopora logani,* which occurs in the lower Lower Silurian (Upper Llandovery, Telychian) to upper Lower Silurian (Lower Wenlock) Anse à Pierre-Loiselle, Limestone Point, and La Vieille formations of northern New Brunswick and the southern Gaspé Peninsula of Québec. *Plasmopora logani* also lacks septa or has weak septal ridges, possesses a coenenchyme similar in appearance to that of our specimen, and has numerical characters that are virtually identical (biometric data for *P. logani*, based on Young and Noble, 1990b, table 4: mean corallum tabularium diameters of 0.96–1.40 mm, mean TuD = 0.30 mm, mean WT = 0.06 mm, TaA:CoA = 0.32; compare with Table 16). Our specimen is identified as *Plasmopora* sp. cf. *P. logani* because of its significantly greater age, and because it is the only known specimen. It is considered to belong to the same lineage as *P. logani.*

Prior to the work of Young and Noble (1990b), *P. logani* from northern New Brunswick and the Gaspé Peninsula had been identified as *Plasmopora follis* or as *Pseudoplasmopora follis.* Young and Noble (1990b, p. 195) discussed the characters that distinguish *P. logani* from *P. follis* and other species.

Plasmopora sp. cf. *P. logani* was listed as *Plasmopora* sp. A by Elias and Young (1992, fig. 2, tables 1, 2).

Occurrence.—Uppermost Ordovician (Gamachian) to lowermost Silurian (?; Lower Llandovery?, lower

Rhuddanian?): Cyrene Formation, northeastern Missouri.

Material described above.—One specimen: UI C-865b, collected by T. E. Savage (labelled "*Lyellia thebesensis,* Edgewood [Formation], Edgewood"), Cyrene Formation, near Edgewood, Pike County, Missouri.

Family **COCCOSERIDIDAE** Kiaer, 1899

Genus **ACIDOLITES**
Lang, Smith, and Thomas, 1940
pro **Acantholithus** Lindström, 1899
(*non* Stimpson, 1858)

Acidolites Lang *et al.,* 1940, p. 13.

Type species.—By original designation: *Acantholithus lateseptatus* Lindström (1899, p. 113, pl. 11, figs. 23–30); probably Ordovician (found in a Pleistocene moraine), Kopparsvik, Gotland, Sweden.

Diagnosis.—"Corallites with partly dilated septa and narrow interseptal spaces crossed by tabulae or with fully dilated septa, no interspaces and no tabulae. Septal trabeculae abut or curve upward into a solid columella of vertical trabeculae. Coenenchyme wide or narrow, with trabeculae arranged to form vertical tubules. Coenenchymal trabeculae variously dilated, resulting in continuous or discontinuous openings, crossed by transverse diaphragms. Trabecular structure evident on surface of corallum as rounded or acute tubercles defining the outlines of coenenchymal tubules and corallites, and in the calices arranged along the edges of septa and clustered on an axial boss terminating the columella." (From Dixon, 1986, p. 29.)

Remarks.—Dixon's (1986, pp. 29, 30) paper on *Acidolites* from eastern North America provides a thorough discussion. His concept of this genus is followed here.

Acidolites species A
Plate 8, figures 5–7

Description.—The single corallum has a high domical growth form. It is extremely small, measuring 8.0 mm wide and 6.6 mm high (Pl. 8, fig. 5).

In transverse section, tabularia are strongly crenulate and very small, with diameters of about 0.65–0.70 mm. Tabularia appear to be wide-spaced. Each tabularium is defined by 12 distinct, thick, contiguous septal trabeculae (Pl. 8, fig. 6); long axis (transverse) of each trabecula is about 50–75% of tabularium radius. Septal trabeculae form the corallite wall, and in some places have exothecal extensions. Septa have upturned spinose tips that form a pseudocolumella in the center of each tabularium; diameters of tips are about 0.050–0.075 mm. In longitudinal section, each tabularium is straight or slightly curved, and is bounded by a thick tabularium on either side. Tabulae are moderately thick, variably and widely spaced (Pl. 8, fig. 7).

In transverse section, the coenenchyme consists of thick irregular trabeculae with diameters of 0.075–0.175 mm; spaces between these trabeculae are present in some places (Pl. 8, fig. 6). In longitudinal section, coenenchymal trabeculae are regular, straight or slightly curved, with flattened bases (Pl. 8, fig. 7).

Discussion.—This corallum has septal and coenenchymal trabeculae that are greatly dilated, and is near one extreme of variation for these characters in *Acidolites.* It is most similar to *Acidolites compactus* Dixon (1986, pp. 39, 40, 42, figs. 7.1–7.7, 10), from member 7 at the top of the Ellis Bay Formation (uppermost Ordovician, Gamachian, to possibly lowermost Silurian, Lower Llandovery, lowermost Rhuddanian) and from the lower Becscie Formation (lower Rhuddanian; Melchin *et al.,* 1991, p. 1861) on Anticosti Island, Québec. The latter species was illustrated by Bolton (1981a, pl. 4, figs. 1, 2) as *Acidolites* sp. Type 2. Like our corallum, *A. compactus* has greatly dilated coenenchymal and septal trabeculae, but its septa are so highly dilated that tabulae are not seen, and its tabularium diameter of 1.1–1.4 mm is much larger.

This corallum is identified as *Acidolites* sp. A. It is not assigned to a new species because only one extremely small corallum is known.

Occurrence.—Uppermost Ordovician (Gamachian): Leemon Formation, southern Illinois.

Material described above.—One specimen: UI C-889b, collected by T. E. Savage (in matrix of specimen labelled "Edgewood [Formation], Thebes"), Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois.

Genus **PROTARAEA**
Milne-Edwards and Haime, 1851

Protaraea Milne-Edwards and Haime, 1851, pp. 146, 208.
[?] *Coccoseris* Eichwald, 1855–1860, p. 2.

Type species.—By subsequent designation (Miller, 1889, p. 201): *Porites vetustus* Hall (1847, p. 71); Trenton Limestone (upper Middle Ordovician), New York, U.S.A.

Diagnosis.—Corallum of thin sheets, commonly encrusting. Corallites close to apparently widely spaced; coenenchyme absent to apparently wide, when present of closely contiguous thick trabeculae perpendicular to surface. Twelve septa of contiguous trabeculae directed steeply upward and filling the lumen. Tabulae absent.

Remarks.—The generic concept we follow is similar to that of Hill (1981, p. F622), except that the material

Table 17.—Biometric data for one corallum of *Protaraea* sp. A (USNM 485778) from the east-central United States. *TaD* = tabularium diameter, *TaA* = tabularium area, *TuD* = tubule diameter, *TC* = thickness of cycles; c.v. = coefficient of variation.

	parameters			
data	*TaD*	*TaA*	*TuD*	*TC*
mean	0.89 mm	0.62 mm^2	0.182 mm	1.92 mm
minimum	0.75 mm	—	0.100 mm	0.60 mm
maximum	1.10 mm	—	0.275 mm	4.05 mm
intracolony c.v.	14.7	—	20.9	—

described here as *Protaraea* sp. A has more broadly spaced tabularia than would be permitted by Hill's definition. In this feature, *Protaraea* sp. A is transitional between *Protaraea* and *Coccoseris;* Sokolov's (1955, p. 466) suggestion that *Coccoseris* is a junior synonym of *Protaraea* may be correct. Neither genus has been analyzed in any detail in the modern literature, however, and the type material requires restudy.

Protaraea species A

Plate 8, figures 8–12

Description.—Laminar corallum growth forms predominate; two of the three coralla form sheets about 0.50–2.25 mm thick, and encrust calcareous algae, brachiopods, and *Halysites alexandricus* (Pl. 8, fig. 12). The one taller corallum (Pl. 8, fig. 8) consists of a vertical stack of horizontal layers with an average thickness of 1.92 mm (Table 17). Layers are separated by sediment inclusions that represent levels where polyps had died prior to colony regeneration.

Contiguous trabeculae fill all tabular and coenenchymal space. Tabularia are crenulate in outline, with adult diameters of 0.75–1.10 mm (Table 17); they are difficult to recognize in transverse sections (Pl. 8, figs. 10, 11). Tabularia appear to be widely spaced; tabularium areas are about 10–20% of corallite areas, but spacing cannot be determined with certainty because of difficulty in discriminating tabularia from coenenchyme. Tabularia are filled with dense polygonal trabeculae; 12 large, regular septal trabeculae with diameters of about 0.225–0.300 mm occur inside each tabularium boundary, with about six smaller trabeculae having diameters of about 0.100–0.275 mm in the center of each tabularium (Pl. 8, fig. 11). In some tabularia, trabeculae are separated from one another by thin, dark lines. Tabularia cannot be distinguished in longitudinal sections.

Corallites lack distinct walls other than the septal trabeculae. In some cases, however, a dark line separates trabeculae in a tabularium from those in the adjacent coenenchyme (Pl. 8, fig. 11). Tabulae are absent.

In transverse section, coenenchyme is composed of polygonal trabeculae with diameters of about 0.100–0.275 mm (Table 17; Pl. 8, figs. 10, 11). Thin, dark lines separate trabeculae in some places (Pl. 8, fig. 11). In longitudinal section, trabeculae are straight or gently curved, with flat or gently rounded bases (Pl. 8, figs. 8, 9) and tips that are pointed and triangulate, or somewhat rounded (Pl. 8, fig. 9).

Discussion.—These coralla are referred to *Protaraea* because their coenenchymes are composed of contiguous trabeculae, and the tabularia are completely filled with trabecular septa and lack tabulae. They are not very similar to any of the species of *Protaraea* that are well documented in the literature, however, because their tabularia are both smaller and much farther apart. This latter character may suggest that these coralla could be better placed in *Coccoseris,* but they have upward-directed septal trabeculae rather than the axially directed septal trabeculae that are apparently typical of that taxon (see *Remarks* under *Protaraea,* pp. 65, 66). These specimens are identified as *Protaraea* sp. A; they are not assigned to a new species because they are few in number and because the type of preservation does not permit complete description and analysis of characters.

Among other species, *Protaraea guijangensis* Lin (1965, pp. 78, 85, pl. 4, fig. 2), from the Upper Ordovician of Guizhou Province, China, may be the most similar to *Protaraea* sp. A. *Protaraea guijangensis* has similar spacing of tabularia, but has somewhat larger tabularia with diameters of about 1.2–1.5 mm. Unfortunately, Lin's illustration shows only a poorly preserved external surface, so detailed comparisons are not possible.

Occurrence.—Uppermost Ordovician (Gamachian): lower Keel Formation, south-central Oklahoma.

Material described above.—Three specimens: USNM 485778, site 23i, USNM 485779c, site 23iii, USNM 485780c, site 23iv, interval 23-2 (*Brevilamnulella* beds), Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma.

Order **HALYSITIDA** Sokolov, 1947

Diagnosis.—Tabulata with thick-walled corallites arranged in uniserial ranks that join to surround lacunae. Septa consist of up to 12 rows of spines and/or longitudinal ridges, rarely more; may be absent. Tabulae usually complete. Adjacent corallites in ranks may or may not be separated by tubules having horizontal or convex tabulae. Corallite increase lateral or interstitial.

Discussion.—Hill (1981, pp. F602, F603) considered halysitids to be a suborder within the Heliolitida on the basis of shared characters including the presence of coenenchyme between corallites and septa typically numbering 12. The former character is almost certainly not homologous, since halysitids having tubules between their corallites are unknown before the upper Caradoc in the Ordovician, apparently having evolved from the non-tubular forms that had first appeared during the Blackriveran (Middle Ordovician). The shared septal number may indicate that halysitids and heliolitids had a common origin, but inclusion within a single order suggests a degree of similarity that is absent between these discrete, internally consistent groups. For these reasons, we follow Scrutton (1985, pp. 34, 36) in recognizing the Halysitida as an order distinct from the Heliolitida.

Family **HALYSITIDAE**
Milne-Edwards and Haime, 1849

Genus **HALYSITES** Fischer von Waldheim, 1828

Alyssites Fischer von Waldheim, 1813, p. 387.
Halysites Fischer von Waldheim, 1828, p. 15.
Schedohalysites Hamada, 1957, p. 401.
Acanthohalysites Hamada, 1957, p. 404.

Type species.—By monotypy: *Tubipora catenularia* Linnaeus (1767, p. 1270); Silurian, Gotland, Sweden.

Diagnosis.—Halysitidae with circular, elliptical, or subquadrate corallites arranged in uniserial ranks. Septa consist of rows of spines and/or longitudinal ridges; may be absent. All or most corallite tabulae are complete. Tubules occur between some or all corallites; tubule tabulae complete.

Discussion.—Our concept of *Halysites* is similar to that put forward by Laub (1979, pp. 271–274). His inclusion of *Schedohalysites* and *Acanthohalysites* as junior synonyms is followed here.

There is one major problem associated with the recognition of *Halysites.* The development of tubules in halysitids is a variable character, and it is not easy to draw a boundary between *Halysites* and *Catenipora,* which completely lacks tubules. Hamada (1957) dealt with this problem by erecting *Schedohalysites* to include those halysitids that possess tubules between some corallites but lack them between others. As Laub (1979, p. 274) noted, however, tubules are not universally present in many species of *Halysites;* their absence from parts of a corallum may be due to developmental stage or to poor preservation. Laub suggested that specimens should be included in *Halysites* if they possess any tubules at all.

A further complication is that certain specimens, including those described below as *Halysites* sp. cf. *H. alexandricus* and *Halysites*? sp. A, possess structures that appear to be tubules that were filled with skeletal material during subsequent growth. Although some species with completely infilled tubules probably evolved from others with open tubules, they would be placed in *Catenipora* according to presently accepted definitions of these genera. Flower (1961, p. 47) considered corals with such features to be "advanced" members of *Catenipora.* Examples in the literature suggest that this problem may involve a number of species (*e.g., Catenipora crassa* Stasinska; see Stasinska, 1967, pp. 43, 44, pl. 7, fig. 1). A classification that would take this into account would necessarily be based on a thorough re-examination of halysitid structure, microstructure, and phylogeny; this is beyond the scope of the present study.

Hill (1981, p. F627) assigned *Halysites* to the subfamily Halysitinae Milne-Edwards and Haime and *Catenipora* to the subfamily Cateniporinae Hamada. We do not recognize those subfamilies because of problems associated with the distinction of *Catenipora* from *Halysites,* as discussed above.

Halysites alexandricus, new species
Plate 9, figures 1–11; Plate 10, figures 1–10;
Plate 11, figures 1–6

Derivation of name.—The species name is derived from Alexander County, Illinois, where the type locality, Section 31 (Thebes North), is situated.

Diagnosis.—*Halysites* with ranks of variable length, commonly one to six corallites between rank junctions. Tabularium dimensions usually with length 1.0–1.8 mm, width 0.7–1.4 mm. Septal spines present, variably developed. Tabulae wide-spaced, usually complete. Tubules small, length 0.1–0.3 mm, width 0.1 – 0.5 mm. Tubules do not occur between every pair of adjacent corallites, are rarely seen in longitudinal sections. Walls between corallites and tubules are thick.

Description of coralla.—Coralla are of low and high bulbous and low domical growth forms (Table 14). Three measured specimens are 33–83 mm wide and 18–43 mm high.

Corallites are arranged in ranks of extremely variable length; commonly one to six corallites between rank junctions (Pl. 9, fig. 4, Pl. 10, fig. 9), occasionally up to 47 corallites without a junction. Density of corallite spacing appears to be related to rank length, with closely spaced corallites occurring in coralla having short ranks. Ranks are broadly curved, and moderately to strongly constricted at intercorallites; they define wide lacunae having subparallel sides. Lacunae are straight, sinuous, or rarely subpolygonal (Pl. 9, fig. 4, Pl. 10, figs. 2, 7, 9, Pl. 11, fig. 3). Rank junctions occur most commonly at lateral corallite walls, rarely at tubules.

In transverse section, corallites are subovate, subelliptical, or subquadrate (Pl. 9, figs. 2, 9, Pl. 10, figs. 2, 6, 7, Pl. 11, figs. 1, 3, 5); they often have flat ends at intercorallites. Tabularia commonly have length 1.0–1.8 mm and width 0.7–1.4 mm (Table 18). Where a rank junction occurs along a lateral corallite wall, the junction corallite is often distorted in the direction of the side rank (Pl. 10, figs. 6, 9, Pl. 11, fig. 3). In longitudinal section, corallites are straight, curved, or somewhat geniculate (Pl. 9, fig. 8, Pl. 10, figs. 3, 5, Pl. 11, figs. 2, 6).

Three distinct "megacorallites" (see Dixon, 1976) are recognized in a transverse section of one specimen (USNM 485781); they are unusually large, with tabularium dimensions up to 3.6 mm by 2.5 mm (Pl. 10, fig. 2). One of the "megacorallites" is subquadrate, with angulate lateral corallite walls, and occurs within a rank that is otherwise normal. The second and third "megacorallites" occur at successive meanders where one rank approaches close to other ranks. The second "megacorallite" is subtriangular, with an angulate lateral wall facing the nearby rank; the opposite lateral wall is normal. The third "megacorallite" is subquadrate, with one of its two angulate lateral walls abutting against the other rank (Pl. 10, fig. 2). In a different specimen (USNM 485800a), several irregularly shaped corallites occur along one side of the corallum (Pl. 10, fig. 9).

Corallite walls are thick or very thick, commonly 0.2–0.4 mm (Table 18). Walls between tabularia and tubules are moderately thick; where tubules are absent, walls between adjacent tabularia are thick. Septa are thorn-like spines that may have broadly thickened bases (Pl. 9, figs. 3, 10). They are rare to abundant, numbering from 0 to 14 in a transverse section of a corallite. Septal length is variable, averaging 22% of tabularium radius but reaching 52% of radius (Table 18). In longitudinal section, septal spines are arranged in rows; they are directed slightly upward, and are straight or curved (Pl. 9, figs. 6, 7).

Tabulae are thin, flat, slightly concave or convex, or irregular. They are usually complete (Pl. 10, figs. 3, 5, 8, 10), rarely incomplete (Pl. 9, fig. 5), and in some cases have crook-shaped, concave depressions. Tabular spacing is broad, variable or regular, averaging about 6 tabulae in 5 mm (Table 18); in some cases spacing shows well-defined cyclomorphic patterns. Tabulae rarely show significant thickening.

In transverse section, tubules are small, commonly with length 0.1–0.3 mm and width 0.1–0.5 mm (Table 18). They are of variable shape: subcircular (Pl. 9, fig. 11, Pl. 10, fig. 1); width greater than length, slit-like or subrectangular (Pl. 9, fig. 1, Pl. 10, fig. 2); rarely length greater than width; in some cases discontinuous and divided into two or three compartments. Tubules are usually aseptate (Pl. 9, fig. 11), but rarely possess short, apparently spinose septa. Lateral walls of tubules are usually thick. Tubules do not occur between every pair of adjacent corallites, and are commonly infilled with skeletal material. Tubules occurring at rank junctions are much larger than usual and are irregular in shape (Pl. 9, fig. 9). Tubules are rarely seen in longitudinal sections. Tubule tabulae are wide-spaced, numbering about 7 in 5 mm, and are flat or slightly concave (Pl. 9, figs. 5, 6, Pl. 11, fig. 4).

Astogeny and corallite increase.—Most observations are based on one serial-sectioned corallum (USNM 485779a). Other specimens are used for comparison.

The protocorallite is not known. In transverse section, corallites occurring in the initial part of a corallum are subelliptical, small, length 0.85–0.95 mm and width 0.5 mm, thick-walled, and possess some short to moderately long septa. Corallites form short ranks that follow the contours of the substrate; ranks are of two to three corallites, initially spreading without joining to surround lacunae. In longitudinal section, bases of corallites occurring in the initial part of a corallum may be flattened, or may conform to the shape of a hard substrate such as a stromatoporoid (Pl. 9, fig. 8). The initial growth of corallites was nearly vertical (Pl. 9, fig. 8) to reptant.

Above the basal part of a corallum, corallites are larger and their septa are commonly longer, though septal development varies vertically throughout the height of a corallite. The form of ranks changes, becoming longer, more sinuous, and subparallel; ranks join to surround elongate lacunae. In longitudinal section, corallites are long, often extending from the base to the upper growth surface (Pl. 9, fig. 8); corallite mortality within a corallum is rarely observed.

Corallite increase may be interstitial (between adult corallites in a rank) or lateral (at the end or side of a rank). Interstitial increase occurred through the expansion of an existing tubule. New corallites in such positions are subquadrate to subelliptical, with proportions similar to those of adult corallites (Pl. 9, figs. 2, 9, Pl. 10, fig. 7). In some cases, new tabularia have quite strongly developed septa (Pl. 9, fig. 9). New tubules were added on either side of each new corallite higher in the colony. In one corallum (UI X-8723), some corallite lumina are connected through gaps in the intercorallite wall, with continuous tabulae occurring between tabularia in some places.

Lateral increase occurred at the ends of ranks or on the lateral margins of adult corallites within ranks. In most cases, no tubule is present between the basal part of the new corallite and the parent corallite; the tubule was added during subsequent growth. In one corallum (USNM 485809; see Pl. 11, fig. 4), however, a new corallite was initiated after the intervening tubule was already in place.

Table 18.—Biometric data for halysitids from the east-central United States. *TaD* = tabularium dimensions (*L* = length, *W* = width), *TaA* = tabularium area, *TuD* = tubule dimensions (*L* = length, *W* = width), *WT* = wall thickness, *LS* = length of septa, *Ta5* = number of tabulae in 5 mm; s.d. = standard deviation, c.v. = coefficient of variation.

species	*parameters*							
data	*TaD (L)*	*TaD (W)*	*TaA*	*TuD (L)*	*TuD (W)*	*WT*	*LS*	*Ta5*
Halysites alexandricus								
mean	1.47 mm	1.03 mm	1.20 mm^2	0.23 mm	0.31 mm	0.305 mm	22%	6.2
range of colony means	1.22–1.68 mm	0.77–1.28 mm	0.74–1.69 mm^2	0.12–0.36 mm	0.19–0.54 mm	0.196–0.394 mm	5–52%	5.1–8.3
s.d. of colony means	0.13 mm	0.15 mm	0.26 mm^2	0.08 mm	0.14 mm	0.052 mm	14%	1.0
c.v. of colony means	8.7	14.1	21.6	36.5	44.8	17.1	63.1	15.5
minimum	0.35 mm	0.60 mm	—	0.05 mm	0.10 mm	0.150 mm	—	3
maximum	2.20 mm	1.70 mm	—	0.45 mm	0.70 mm	0.500 mm	—	10
mean intracolony c.v.	14.1	13.7	—	43.0	31.1	12.4	—	16.5
no. of coralla studied	20	20	20	7	7	16	11	15
Halysites sp. cf. *H. alexandricus*								
mean	1.38 mm	0.85 mm	0.92 mm^2	0.14 mm	0.12 mm	0.186 mm	48%	11.9
minimum	1.10 mm	0.65 mm	—	0.10 mm	0.10 mm	0.150 mm	—	10
maximum	1.55 mm	1.35 mm	—	0.20 mm	0.20 mm	0.275 mm	—	14
intracolony c.v.	8.7	16.5	—	26.9	34.9	21.5	—	14.3
no. of coralla studied	1	1	1	1	1	1	1	1
Halysites? sp. A								
mean	2.49 mm	1.44 mm	2.82 mm^2	—	—	0.210 mm	28%	11.3
minimum	2.00 mm	1.25 mm	—	—	—	0.150 mm	—	10
maximum	2.85 mm	1.70 mm	—	—	—	0.250 mm	—	12
intracolony c.v.	9.6	9.7	—	—	—	15.2	—	10.6
no. of coralla studied	1	1	1	—	—	1	1	1
Catenipora lawrencica								
mean	0.57 mm	0.36 mm	0.16 mm^2	—	—	0.164 mm	19%	13.2
range of colony means	0.49–0.70 mm	0.29–0.47 mm	0.11–0.26 mm^2	—	—	0.150–0.175 mm	—	—
s.d. of colony means	0.08 mm	0.08 mm	0.06 mm^2	—	—	0.013 mm	—	—
c.v. of colony means	14.2	21.4	37.7	—	—	22.0	—	—
minimum	0.35 mm	0.20 mm	—	—	—	0.100 mm	—	11
maximum	0.85 mm	0.60 mm	—	—	—	0.225 mm	—	16
mean intracolony c.v.	11.8	13.0	—	—	—	22.0	—	14.4
no. of coralla studied	6	6	6	—	—	4	1	1

Microstructure.—Corallite walls are fibrous, consisting of an inner and an outer layer. Relative thicknesses of the two layers are variable, but they are usually approximately equal. The outer layer of the wall covers the outer margin of each rank along the edges of both corallites and tubules (Pl. 9, figs. 2, 9, 11). It is usually dark in color, and has growth lamellae oriented parallel to the wall in transverse section. In longitudinal section, lamellae are directed obliquely outward with height in the corallum at an angle of about 20° from vertical, presumably parallel with the former position of polyp tissue (Pl. 9, figs. 6, 7). In longitudinal sections of some corallites, the lamellae of the outer wall interdigitate with the inner wall material.

The inner layer of the wall is paler than the outer one. In transverse sections of corallites, fibers in this layer are seen in oblique cross section, and appear approximately parallel to the wall (Pl. 9, figs. 3, 10). In longitudinal sections they are elongate, directed upward adaxially at angles from the horizontal of 0–60°, usually 30–45° (Pl. 9, figs. 6, 7). In the intercorallite area, the inner wall continues as a pale surface layer (Pl. 9, figs. 2, 11); a darker area occurs farther inside the intercorallite, but other pale areas are seen around some tubules (Pl. 9, fig. 11). In many specimens the darker intercorallite wall material includes poorly defined fibrous bundles (Pl. 9, figs. 2, 11) that probably represent the "balken" of Fischer-Benzon (1871, pp. 14, 15). Septal spines are thorn-like, apparently fibrous, and are embedded in the inner corallite wall; they are darker than that wall, usually about the same color as the outer wall (Pl. 9, figs. 2, 6, 7, 10). The inner wall is often deflected into the lumen around a septal spine (Pl. 9, figs. 10, 11).

Both wall layers are commonly affected by diagenetic alteration. With low-level alteration, the inner wall may take on a lamellar appearance with lamellae parallel to those of the outer wall. With a higher degree of diagenesis, both walls may be composed of continuous fibers oriented perpendicular to the wall in transverse section, or may even take on a pseudotrabecular appearance.

Corallite tabulae are dark-colored and are embedded in the axial edges of the inner corallite wall (Pl. 9, figs. 6, 7). Tabular structure is indistinct, but appears to consist of fibers oriented perpendicular to the plane of each tabula. Tubule tabulae are also dark in color, and abut the edges of the intercorallite walls (Pl. 9, fig. 6); their structure cannot be distinguished.

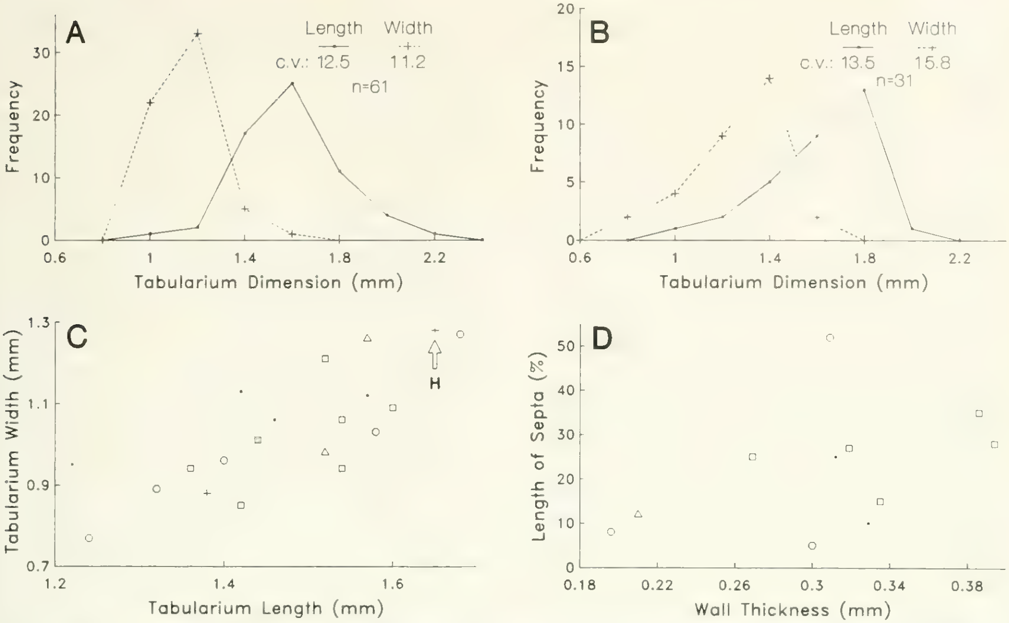
Intraspecific variation.—This species is variable in many characters, such as septal development and the length and arrangement of ranks. The fragmentary nature of many specimens limits the analysis of much of this variation, however, and the data are insufficient for determination of interlocality differences in most characters.

Frequency distributions for tabularium dimensions in two coralla are approximately normal, with length and width having similar curves in each example (Text-fig. 19A, B). Size ranges for both dimensions tend to be relatively broad. The holotype (USNM 485781) has three "megacorallites" that are irregular in outline and about twice the dimensions of normal corallites (*e.g.*, Pl. 10, fig. 2); these are not included in the frequency distribution for the specimen.

A graph of tabularium mean length and width (Text-fig. 19C) indicates that the ratio of these dimensions remains constant at about 1.3–1.4, regardless of the mean corallite size for a corallum. At each locality for which a large number of specimens is available, such as Sections 23 (Lawrence Quarry) and 15 (Calumet), there is a substantial range of mean tabularium dimensions. No locality stands out as significantly different from the others in these characters.

Septal length appears to be related to wall thickness, with long septa occurring only in those coralla that have thick corallite walls (Text-fig. 19D). These characters show some interlocality variation; septa are generally long at Section 23, and are variably developed at Section 15. Septal length and wall thickness do not correlate with tabularium dimensions.

Discussion.—These coralla are assigned to a new species, *Halysites alexandricus.* This species is the oldest representative of *Halysites* documented from North America. Worldwide, members of this genus are rare in uppermost Ordovician to lowest Silurian strata, but three other species have characters that are similar to those of *H. alexandricus.* The oldest definite member of this genus is *Halysites praecedens* Webby and Semeniuk (1969, pp. 349–353, figs. 2–6), from the upper Bowan Park Group and upper Canomodine Limestone of New South Wales, Australia (Ordovician, upper Caradoc–lower Ashgill; Webby *et al.*, 1981, pl. 1). It has tabularium dimensions of about 1.2–2.0 mm by 1.2–1.6 mm, rectangular tubules, and flat tabulae. *Halysites* sp. of Hall (1975, p. 89, fig. 12, pl. 5, figs. b, c), from the Uralba Beds of New South Wales (Upper Ordovician, Ashgill), has corallites with tabularium dimensions of about 1.4–1.7 mm by 0.8–1.0 mm, arranged in short ranks. *Halysites priscus* Klaamann (1966, p. 93, pl. 22, figs. 5–7), from the Juuru Stage of Estonia (lower Lower Silurian, Lower Llandovery), has tabularium dimensions of 1.6–1.8 mm by 1.4–1.55 mm, and rectangular tubules. All three of these species differ from *H. alexandricus* by having smaller or absent corallite septa, much thinner walls between corallites



Text-figure 19.—Intraspecific variation in *Halysites alexandricus*. **A, B**, Tabularium size-frequency distributions for selected coralla: A, USNM 485781 (holotype), Section-interval 31-1 (Thebes North); B, USNM 485809, Section-interval 37-1 (Essex). Each graph represents a single transverse section; tabularium length and width are shown separately; n = number of tabularia, c.v. = coefficient of variation. **C**, Relationship between mean tabularium width and mean tabularium length for transverse sections from 20 coralla; H = USNM 485781 (holotype). **D**, Relationship between length of septa as a percentage of tabularium radius and mean wall thickness for transverse sections from 11 coralla. Symbols for Section-intervals in C and D: □ 23a-1, 23-2 (Lawrence Quarry); + 31-1 (Thebes North); ○ 15-1 (Calumet); △ 37-1 (Essex); ■ all other Section-intervals.

and tubules, and tubules that are more abundant and that were initiated lower in the growth of the adjacent corallites.

Patterns of increase observed in *H. alexandricus* are notable for their variability (see *Astogeny and corallite increase,* above). Interstitial increase through expansion of an existing tubule is consistent with forms described from Ordovician and Silurian species of *Halysites* by Webby and Semeniuk (1969, pp. 354, 355, fig. 8a) and by Webby (1975, p. 35, fig. 5), but the connections between corallite lumina in one specimen of *H. alexandricus* suggest that axial increase (*cf.*, Lee and Elias, 1991, p. 193, figs. 1, 2) may also have occurred. Lateral increase took place either with or without an intervening tubule; the former pattern is the same as that reported by Webby and Semeniuk (1969, p. 355, fig. 8b) and Webby (1975, p. 34, fig. 4) for Ordovician and Silurian species of *Halysites,* whereas the latter was suggested by Buehler (1955, p. 14) and Hamada (1959, p. 276) as the most likely mode of increase for all halysitids. The occurrence of this range of types of increase in one species indicates that it could vary styles of growth, probably in response to local conditions.

"Megacorallites," which occur rarely in *H. alexandricus,* are apparently rare among halysitid corals in general. They have been previously reported in two specimens of *Catenipora* from the Lang River Formation (Upper Ordovician) on Somerset Island in the Canadian Arctic. The "megacorallites" in one corallum from Somerset Island are mostly subcircular in transverse section, and commonly occur at the center of tri- or quadripartite rank divergences (Dixon, 1976, pl. 1, figs. 1, 2a, 2b). "Megacorallites" in the other specimen are more commonly subelliptical, and occur within uniserial ranks (Dixon, 1976, pl. 1, figs. 3, 4a–

c). The paleobiologic significance of "megacorallites" is uncertain (see Dixon, 1976, p. 918). We consider them to be anomalous features; as such they are not given weight in taxonomy (*cf.*, Dixon, 1976, p. 920).

Halysites alexandricus was listed and illustrated by Elias and Young (1992, figs. 2, 3e, 3f, tables 1, 2) as *Halysites* n. sp. A. A similar younger species, *Halysites* sp. cf. *H. alexandricus* from the Sexton Creek Limestone of southern Illinois, is described below.

Occurrences.—Uppermost Ordovician (Gamachian): Cason Shale, western north-central Arkansas; Leemon Formation, southern Illinois and southeastern Missouri. Uppermost Ordovician (Gamachian) to lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): lower and upper Keel Formation, south-central Oklahoma. Uppermost Ordovician (?; Gamachian?) to lowermost Silurian (Lower Llandovery, lower Rhuddanian): Wilhelmi Formation, northeastern Illinois; lower Mosalem Formation, northwestern Illinois. Lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): Kissenger Limestone Member, Bryant Knob Formation, northeastern Missouri.

Holotype.—USNM 485781 (Pl. 10, figs. 2–4), interval 31-1, Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois.

Paratypes.—Four specimens: USNM 485782 (Pl. 9, figs. 1–3), site 23i, USNM 458778 (Pl. 9, figs. 4–6), site 23ii, interval 23-2 (*Brevilamnulella* beds), Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; USNM 485783 (Pl. 10, figs. 7, 8), interval 15-1, Kissenger Limestone Member, Bryant Knob Formation, Section 15 (Calumet), Pike County, Missouri; UI X-8723 (Pl. 11, figs. 5, 6), collected by T. E. Savage (labelled "*Halysites catenularia,* 1 mi. below otc. of Channahon ls."), Wilhelmi Formation, 3.2 km south of Channahon, Will County, Illinois.

Other material described above.—38 specimens: USNM 485779a, 485784, site 23iii, USNM 485780a, 485785b, 485786, site 23iv, interval 23-2 (*Brevilamnulella* beds), USNM 485787, 485788, site 23i, USNM 485789, 485790, site 23ii, interval 23-3, USNM 423421 (paratype of *Keelophyllum oklahomense* is attached to *Halysites alexandricus*), 485791, 485792, collected by R. J. Elias and R. J. McAuley in 1983, interval 23a-1 of McAuley and Elias (1990, p. 53, fig. 2), Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; USNM 485793, interval 24-3, Keel Formation, Section 24 (Coal Creek), Pontotoc County, Oklahoma; USNM 485794, interval 25-1, Keel Formation, Section 25 (Hunton), Coal County, Oklahoma; USNM 485795, collected by W. W. Craig, interval 33-1, Cason Shale, Section 33 (Buffalo River), Searcy County, Arkansas; USNM 485796, interval 31-1, Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois; UI C-886b, collected by T. E. Savage (labelled "Edgewood [Formation], near Gale, Ill."), Leemon Formation, Gale Section, Alexander County, Illinois; USNM 423401 (*H. alexandricus* is in matrix enclosing *Streptelasma leemonense*), collected by R. J. Elias and R. J. McAuley in 1983, interval 20-3, Leemon Formation, Section 20 (Short Farm), Cape Girardeau County, Missouri; USNM 485797, interval 18-2, USNM 485723c, interval 18-3, Kissenger Limestone Member, Bryant Knob Formation, Section 18 (Kissenger), Pike County, Missouri; USNM 485727b, 485798, 485799, 485800a, 485800b, 485801–485803, interval 15-1, Kissenger Limestone Member, Bryant Knob Formation, Section 15 (Calumet), Pike County, Missouri; USNM 485804, 485805, interval 14-1, Kissenger Limestone Member, Bryant Knob Formation, Section 14 (Higginbotham Farm), Pike County, Missouri; USNM 485806–485809, interval 37-1, Wilhelmi Formation, Section 37 (Essex), Kankakee County, Illinois; UI C-157, collected by H. F. Crooks (labelled "*Halysites catenulatus,* loc. A-1c"), UI C-1587b, collected by T. E. Savage (labelled "*Halysites catenularia,* 1 mi. below otc. of Channahon ls."), Wilhelmi Formation, 3.2 km south of Channahon, Will County, Illinois; USNM 485810, 485811, interval 32-1z, Mosalem Formation, Section 32 (Thomson East), Carroll County, Illinois.

Halysites species cf. **H. alexandricus**, new species
Plate 11, figures 7–9

Description.—Ranks are moderately long, consisting of one to six corallites. They are straight or broadly curved, and moderately constricted at intercorallites. Rank junctions occur at lateral corallite walls, or very rarely at tubules. Lacunae are broad, elongate or subpolygonal (Pl. 11, fig. 7). In transverse section, corallites are subelliptical, with tabularium dimensions commonly having length 1.25–1.55 mm and width 0.75–0.90 mm (Table 18). Where a rank junction occurs along a lateral corallite wall, the junction corallite is usually distorted in the direction of the side rank (Pl. 11, fig. 8). In longitudinal section, corallites are straight or slightly curved (Pl. 11, fig. 9).

Corallite walls are thick, averaging about 0.2 mm (Table 18). They are composed of two layers: a thinner, dark outer layer and a thicker, pale inner layer. Microstructure could not be determined because of recrystallization. Walls between tabularia and tubules are thick; where tubules are absent, walls between adjacent tabularia are very thick (Pl. 11, fig. 7). Septal spines are slender and long, averaging 48% of tabularium radius (Table 18). Tabulae are flat to strongly concave, usually complete, and irregularly and densely spaced, averaging about 12 in 5 mm (Table 18).

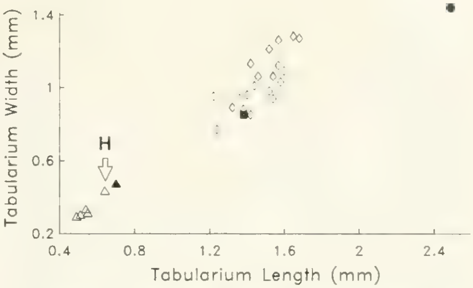
In transverse section, tubules are usually subelliptical and are very small, measuring 0.1–0.2 mm by 0.1–0.2 mm (Table 18). Most tubules are infilled with skeletal material. A tubule does not occur between every pair of adjacent corallites. Lateral walls of tubules are thick. Tubules are not seen in longitudinal section (Pl. 11, fig. 9).

Discussion.—This corallum bears a high degree of similarity to the older *Halysites alexandricus,* which occurs in uppermost Ordovician and lowermost Silurian rocks of the east-central United States. This similarity probably reflects an ancestor–descendent relationship. The only significant difference between these forms is that tabulae in this corallum are commonly strongly concave and are more closely spaced than in any specimen of *H. alexandricus* (see Table 18). Tabularium dimensions in this corallum are smaller than those of most specimens of *H. alexandricus,* but still within the range for the latter species (see Text-fig. 20).

This corallum is identified as *Halysites* sp. cf. *H. alexandricus* because of the close similarity to *H. alexandricus,* as discussed above. The single specimen does not provide sufficient information for recognition of a new species. It was referred to as *Halysites* sp. cf. *H.* n. sp. A by Elias and Young (1992, fig. 2).

Occurrence.—Lower Lower Silurian (Lower? Llandovery, upper Rhuddanian?): Sexton Creek Limestone, southern Illinois.

Material described above.—One specimen: UI C-1346a, collected by T. E. Savage (labelled "*Halysites catenulatus*"), Sexton Creek Limestone, Sexton Creek, Alexander County, Illinois.



Text-figure 20.—Relationship between mean tabularium width and mean tabularium length in halysitid species from the east-central United States. Symbols for species: ◇ *Halysites alexandricus;* n (number of coralla) = 20; ■ *Halysites* sp. cf. *H. alexandricus;* n = 1; ● *Halysites*? sp. A; n = 1; △ *Catenipora lawrencica;* Section 23 (Lawrence Quarry); n = 5; H = USNM 485780b (holotype); ▲ *C. lawrencica;* Section-interval 14-1 (Higginbotham Farm); n = 1.

Halysites? species A
Plate 12, figures 1, 2

Description.—Ranks are moderately long, consisting of one to more than four corallites. Ranks are straight or slightly curved, and moderately constricted at intercorallites; they surround broad, subpolygonal lacunae. Rank junctions occur at lateral corallite walls. In transverse section, corallites are subelliptical and large, with tabularium dimensions commonly having length 2.3–2.7 mm and width 1.3–1.6 mm (Table 18). A corallite having a rank junction along its lateral wall is usually distorted in the direction of the side rank (Pl. 12, fig. 1).

Corallite walls are thick, about 0.2 mm (Table 18); microstructure cannot be determined because of recrystallization. Intercorallites are very thick in the direction of rank extension. Septal spines are common to abundant, upturned, thick, and of medium length, averaging 28% of tabularium radius (Table 18; Pl. 12, fig. 2). Tabulae are flat or irregular, mostly complete, and of variable thickness, with some being quite thick (Pl. 12, fig. 2). Tabulae are closely spaced, averaging about 11 in 5 mm (Table 18). Some tabulae bear short to long, vertically oriented spines on their upper surfaces; spines are most abundant on thickened tabulae (Pl. 12, fig. 2).

Tubules are not observed. The central parts of many intercorallites, however, have the appearance of small, broad tubules that have been filled in, either by the growth of skeletal material or by recrystallization (Pl. 12, fig. 1).

Discussion.—Assignment of this corallum to *Halysites* is questionable because open tubules were not observed between the corallites. Nevertheless, the structures that are present in the intercorallite walls may represent tubules that were filled in during later skeletal growth or by recrystallization. In the past, some species with intercorallites of similar character have been placed in *Catenipora;* a revision of these genera is needed to determine where the boundary between them should be placed (see *Discussion* under *Halysites,* p. 67).

This corallum is similar to Silurian halysitids that have been assigned by different authors to *Halysites gotlandicus* Yabe (1915) (= *Catenipora gotlandica*). The original description of *H. gotlandicus* from Korpklint, Gotland, Sweden (probably Upper Visby or Högklint beds: upper Lower Silurian, Lower Wenlock; Laufeld and Jeppsson, 1976, fig. 1), indicates that it has large corallites with dimensions of 1.9–2.1 mm by 1.6–1.7 mm, and short septal spines, but lacks tubules (Yabe, 1915, pp. 34(10), 35(11), pl. 7(3), figs. 1, 2; Buehler, 1955, p. 57). Yabe's illustrated transverse section, however, appears to show tubules that have been filled with skeletal material.

Catenipora cf. *gotlandica* of Klaamann (1966, pp. 41, 42, fig. 18, pl. 6, fig. 6), from the Juuru Stage of Estonia (lower Lower Silurian, Lower Llandovery), is most similar to our corallum. It has irregular tabulae, some of which have spines on their surfaces, and well-developed septal spines, but differs by having smaller corallites with dimensions of about 1.7–2.0 mm by 1.3–1.5 mm (inside?), and smaller intercorallites that probably lack infilled tubules. *Catenipora gotlandica*, as described and illustrated by Klaamann (1966, pp. 42, 43, fig. 19) from the Upper Llandovery of Gotland, the Juuru Stage of Estonia, and the Llandovery to Wenlock of Arctic Russia and the Siberian Platform, is less similar. It has intercorallites that are short in the direction of rank extension, and lacks tabular spines.

Catenipora gotlandica was described and illustrated from the mid-Llandovery Brassfield Formation of Ohio by Laub (1979, pp. 290–295, pl. 9, fig. 8, pl. 33, figs. 1, 2, pl. 42, fig. 2). It has smaller corallites than our corallum, with dimensions of 1–2 mm by 1.2 mm, and smaller intercorallites, but has large septa and appears to have sporadically developed infilled tubules.

The corallum we describe here is clearly differentiated from the other halysitid species occurring in the study region by its much larger corallite dimensions (Text-fig. 20). It is identified as *Halysites*? sp. A because of the problems outlined above, and because only one fragmentary specimen was found. *Halysites*? sp. A was referred to as *Halysites* sp. A by Elias and Young (1992, fig. 2).

Occurrence.—Lower Lower Silurian (Lower? Llandovery, upper Rhuddanian?): Sexton Creek Limestone, southern Illinois.

Material described above.—One specimen: UI C-1346b, collected by T. E. Savage (labelled "*Halysites catenulatus*"), Sexton Creek Limestone, Sexton Creek, Alexander County, Illinois.

Genus **Catenipora** Lamarck, 1816

Catenipora Lamarck, 1816, p. 206.
Palaeohalysites Chernyshev, 1941, p. 36.
Quepora Sinclair, 1955, p. 96.
[?] *Eocatenipora* Hamada, 1957, p. 398.

Type species.—By subsequent designation (Lang *et al.*, 1940, p. 33): *Catenipora escharoides* Lamarck (1816, p. 207); Silurian, Gotland, Sweden.

Diagnosis.—Halysitidae with circular to elliptical corallites arranged in uniserial ranks. Septa consist of longitudinal ridges and/or rows of spines; may be absent. All or most corallite tabulae are complete. Tubules are absent.

Remarks.—The concept of *Catenipora* used here is similar to that of Laub (1979, pp. 288–290). We follow him in the synonymization of *Palaeohalysites* and *Quepora*, and the questionable synonymization of *Eocatenipora*. Problems associated with the distinction of *Catenipora* from *Halysites* are addressed elsewhere (see *Discussion* under *Halysites*, p. 67).

Catenipora lawrencica, new species
Plate 12, figures 3–11

Derivation of name.—The species name is derived from the type locality, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma.

Diagnosis.—*Catenipora* with ranks usually of one to four corallites; most rank junctions occur at intercorallites. Tabularium dimensions commonly with length 0.4–0.7 mm, width 0.3–0.5 mm. Ranks strongly constricted at intercorallites. Corallite walls thick, septal spines common. Tabulae are complete.

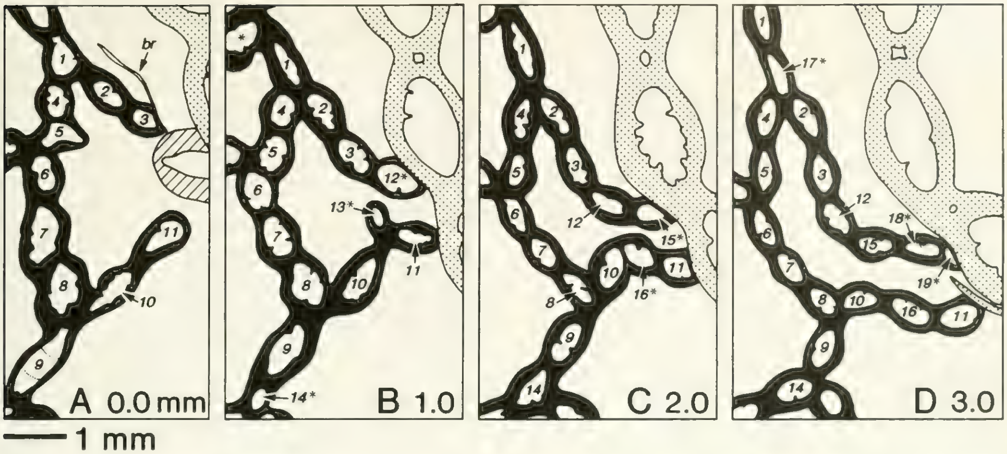
Description of coralla.—Coralla are small, and commonly occur as encrusters on *Halysites alexandricus*. Growth forms cannot be determined since all specimens are bound in matrix.

Ranks commonly consist of one to four corallites, but are longer in some cases (Pl. 12, figs. 5, 10, 11). Ranks are broadly curved and strongly constricted at intercorallites. They enclose lacunae that are small and polygonal to subpolygonal, or elongate, narrow, and sinuous in some places. Rank junctions usually occur at intercorallites (Pl. 12, fig. 5), but may occur at lateral corallite walls (Pl. 12, fig. 10). In transverse section, corallites are subelliptical or subovate, with flat or rounded ends at intercorallites (Pl. 12, figs. 6, 10, 11). They are small, with tabularium dimensions commonly having length 0.4–0.7 mm and width 0.3–0.5 mm (Table 18). Corallites are straight, curved, or slightly geniculate in longitudinal section (Pl. 12, figs. 3, 7).

Corallite walls are thick, usually 0.1–0.2 mm (Table 18). Walls are composed of two layers: a thinner, dark outer layer and a thicker, pale inner layer (Pl. 12, fig. 9). Microstructure cannot be determined because of recrystallization. Intercorallite walls are thin to moderately thick. In transverse section, the central part of an intercorallite in some cases comprises a dark transverse line (Pl. 12, fig. 9). Septa consist of moderately thick spines, with length averaging 19% of corallite radius (Table 18); they are common where preserved (Pl. 12, fig. 6). In longitudinal section, septal spines are arranged in rows (Pl. 12, fig. 3).

Tabulae are flat, slightly concave or slightly convex, and complete (Pl. 12, figs. 3, 7). Spacing is variable but moderately close, averaging about 13 tabulae in 5 mm (Table 18). Tabulae were probably thin prior to recrystallization.

Astogeny and corallite increase.—Most observations are based on one serial-sectioned corallum (holotype



Text-figure 21.—**A–D**, Serial transverse sections illustrating corallite increase in a corallum of *Catenipora lawrencica;* USNM 485780b (holotype), Section-interval 23-2 (Lawrence Quarry) (see also Pl. 12, figs. 3–6). Corallite walls and septa are solid, tabulae are finely stippled; a rank of *Halysites alexandricus* is coarsely stippled, a possible corallite of *Aulopora* is hachured, *br* = brachiopod shell; scale bar is shown. Heights in mm are above an arbitrary datum within a mature part of the corallum; numbers in italics represent individual corallites; an asterisk indicates the first appearance of a particular corallite.

USNM 485780b). Other specimens are used for comparison.

The protocorallite is not known. The lowest known stages of corallum growth have thick-walled, septate corallites that are not distinguishable from those occurring higher up. Ranks in the lower part of the corallum are short and straight or slightly curved, commonly composed of one to three corallites. They are initially spreading and do not join to form lacunae. Higher in the corallum, ranks are subparallel, longer and more sinuous, commonly having two to four corallites. Ranks join to surround subpolygonal lacunae that become more elongate with height. The shape of ranks may vary depending on whether lateral growth was blocked by large skeletal grains (Text-fig. 21). In longitudinal section, some corallites extend through much of the height of the corallum.

Corallite increase may be interstitial (between adult corallites in a rank) or lateral (at the end or side of a rank). Interstitial increase apparently occurred through fission of the intercorallite wall. New corallites produced by interstitial increase are separated by thin walls from the adult corallites on either side (Text-fig. 21B, C, note corallites 10, 11, 16). In transverse section, such new corallites are initially more broadly elliptical, and are shorter in the long axis than are adult corallites; they expanded rapidly to adult size and shape (Text-fig. 21C, D, note corallite 16).

Lateral increase occurred at the free ends of ranks, more rarely at the sides of ranks. At the end of a rank, a new corallite appeared through the fission of the end wall of the parent individual (Text-fig. 21D, note corallite 19). The intercorallite wall between the new corallite and the parent is thin, but of normal appearance. New corallites in such locations expanded rapidly, both where rank ends were free and where they adhered to large skeletal grains (Text-fig. 21C, D). At the side of a rank, a new corallite is located beside an intercorallite (Text-fig. 21B, corallite 13).

Partial mortality of colony growth surfaces was not observed. A single corallite, however, viewed in longitudinal section, exhibits a constriction followed by rejuvenation from within the calice (Pl. 12, figs. 3, 4).

Discussion.—The coralla described above are assigned to a new species, *Catenipora lawrencica.* This is one of the older members of an important group of small-corallite *Catenipora* species that developed during an evolutionary radiation from the latest Ordovician through the earliest Silurian. Species in this group occur in Asia, central and eastern North America, and the Baltic region. All have tabularium dimensions of less than 1.5 mm by 1.2 mm and rank junctions occurring mostly at intercorallites, and many have well-developed septa and polygonal or broad lacunae. Although the shared characters allow these corals to be readily recognized as members of a group, the literature includes many names for what is probably a limited number of species; this prevents the compilation of a valid list at present.

Other than *Catenipora lawrencica,* the well-documented Ordovician members of this group all occur in Asia. These include *Catenipora* (*Catenipora*?) *minima* Yü (1960, pp. 83, 98, pl. 9, figs. 6, 7) from the Upper Ordovician of western Zhejiang Province, China, *Catenipora zhejiangensis* Yü as described by Lin and Chow (1977, pp. 160, 161, pl. 40, figs. 2, 3) from the Upper Ordovician (Ashgill) of Zhejiang and Jiangxi provinces, China, and *Catenipora capilliformis* Kokscharskaya (in Volkova *et al.,* 1978, pp. 30, 31, pl. 3, fig. 1) from the Upper Ordovician Barannskiy Stage of southern Verkhoyan, Siberian region, Russia. These three species are very similar to one another and may be conspecific; they are distinguished from *C. lawrencica* by their larger corallites with tabularium dimensions of about 0.6–0.9 mm by 0.5–0.8 mm, and a lower degree of constriction at each intercorallite.

Most of the many small-corallite *Catenipora* species described and illustrated from the Baltic region are from the lower Lower Silurian (Upper Llandovery) or upper Lower Silurian (Wenlock). Among the few earlier occurrences, *Catenipora escharoides* has been listed by Aarhus (1982, p. 44) from the latest Ordovician of the Oslo region, Norway. It also occurs in the upper Rytteråker Formation (Llandovery 7b: Upper Llandovery, Telychian; Worsley *et al.,* 1983, fig. 5) and in the lower and middle Vik Formation (Llandovery 7c: Telychian; Worsley *et al.,* 1983, fig. 5) of Ringerike, Norway (Aarhus, 1982, p. 44, pl. 2, fig. 6), and in the Lower and Upper Visby beds of Gotland, Sweden (uppermost Llandovery–Lower Wenlock; Laufeld and Jeppsson, 1976, fig. 4) (Stasinska, 1967, pp. 44, 45, pl. 3, figs. 5–8). *Catenipora escharoides* is differentiated from *C. lawrencica* by its much larger corallites with tabularium dimensions of about 1.0–1.5 mm by 0.9–1.2 mm, much larger septa, and small, regular lacunae. *Catenipora minuta* Stasinska (1967, p. 48, pl. 6, fig. 2), from the Upper Llandovery of Ringerike (Llandovery 7), is very similar to *C. escharoides* and may be conspecific with it.

Another early Baltic species is *Catenipora arctica* Chernyshev, as described and illustrated by Klaamann (1966, pp. 40, 41, pl. 22, fig. 8) from the Lower Llandovery Juuru Stage of Estonia. It has thick walls and subpolygonal lacunae, but is distinguished from *C. lawrencica* by its larger corallites with tabularium dimensions of 0.8–1.0 mm by 0.54–0.66 mm. *Catenipora arctica* also occurs in the Llandovery of Taimyr, northern Russia (Klaamann, 1966, p. 41).

Of the later members of the small-corallite *Catenipora* group from the Baltic, the species most similar to *C. lawrencica* is probably *Catenipora panga* Klaamann (1961; 1966, pp. 52, 53, pl. 14, figs. 7, 8), from the Adavere and Jaani stages of Estonia (Upper Llandovery–Wenlock). *Catenipora panga* also has constricted intercorallites and subpolygonal lacunae, but is distinguished from *C. lawrencica* by its larger corallites with tabularium dimensions of 0.9–1.1 mm by 0.7–0.8 mm, and irregular tabulae. *Catenipora jarviki* Stasinska (1967, pp. 47, 48, pl. 2, fig. 1), from the Wenlock of Gotland, Sweden (Visby beds?), is also similar to *C. lawrencica,* but has diamond-shaped corallites that are larger (tabularium dimensions 0.6–0.9 mm by 0.4–0.5 mm) and arranged in longer ranks.

Most of the described North American small-corallite *Catenipora* species are Late Llandovery or Wenlock. Bolton (1981a, pl. 1, figs. 4, 5), however, illustrated two coralla identified as *Catenipora* sp. from the Ellis Bay Formation of Anticosti Island, Québec (member 5 of Bolton: uppermost Ordovician, Gamachian; Petryk, 1981, fig. 4). These specimens possess polygonal to subpolygonal ranks and constricted intercorallites. They differ from *C. lawrencica* by having significantly larger corallites with long tabularium dimensions greater than 1 mm. Other coralla from the Ellis Bay Formation, Becscie Formation (Lower Llandovery, Rhuddanian), and Jupiter Formation (Middle–Upper Llandovery, upper Aeronian–Telychian; Barnes, 1988, fig. 2) on Anticosti Island were described as *Halysites catenularia micropora* Whitfield by Twenhofel (1928, p. 125). Twenhofel's material, deposited at the Geological Survey of Canada and the Yale Peabody Museum, is unfortunately lost (Bolton, written commun., 1991; White, written commun., 1991), but his description of corallites less than 1.0 mm by 0.5 mm suggests that it may have included specimens similar to *C. lawrencica.*

Six of the seven specimens of *C. lawrencica* are from the Keel Formation at Section 23 (Lawrence Quarry). These are very consistent with one another in most of the important morphologic characters, but they differ somewhat from the single fragmentary corallum from the Bryant Knob Formation at Section 14 (Higginbotham Farm). The latter specimen has larger corallites (Text-fig. 20), and also appears to have longer and thicker septa. These differences may be related to geographic and stratigraphic separation, and are not sufficient to place the specimen from Section 14 in another species. *Catenipora lawrencica* was referred to as *Catenipora* n. sp. A by Elias and Young (1992, fig. 2, tables 1, 2).

Occurrences.—Uppermost Ordovician (Gamachian): lower Keel Formation, south-central Oklahoma. Lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): Kissenger Limestone Member, Bryant Knob Formation, northeastern Missouri.

Holotype.—USNM 485780b (Pl. 12, figs. 3–6), site 23iv, interval 23-2 (*Brevilamnulella* beds), Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma.

Paratypes.—Two specimens: USNM 485785c (Pl. 12, figs. 7–10), site 23iv, interval 23-2 (*Brevilamnulella* beds), Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma. USNM 485812b (Pl. 12, fig. 11), interval 14-1, Kissenger Limestone Member, Bryant Knob Formation, Section 14 (Higginbotham Farm), Pike County, Missouri.

Other material described above.—Four specimens: USNM 485813, site 23i, USNM 485779b, site 23iii, USNM 485814, site 23iv, interval 23-2 (*Brevilamnulella* beds), USNM 485815, collected by R. J. Elias and R. J. McAuley in 1983, interval 23a-1 of McAuley and Elias (1990, p. 53, fig. 2), Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma.

Order **FAVOSITIDA** Wedekind, 1937

Suborder **FAVOSITINA** Wedekind, 1937

Superfamily **FAVOSITICAE** Dana, 1846

Family **FAVOSITIDAE** Dana, 1846

Subfamily **FAVOSITINAE** Dana, 1846

ex Favositidae Dana, 1846, p. 116; *nom. transl.* Milne-Edwards and Haime, 1851, p. 230.
Palaeofavositinae Sokolov, 1950a, pp. 164, 165.
Paleofavositinae Sokolov, 1950a; *nom. correct.* Hill, 1981, p. F546.

Diagnosis.—Favositidae with septa spinose or absent. Longitudinal rows of pores located in wall faces and/or in corners.

Discussion.—The Paleofavositinae was previously distinguished from the Favositinae solely on the basis of pore position (Hill, 1981, pp. F541, F546); all other characters are similar between the nominate genera. Since pore form and placement are extremely variable within *Paleofavosites*, however, it is not feasible to continue to separate these subfamilies. Members of *Paleofavosites* may possess combinations of mid-wall pores, simple corner pores, and solenia (funnel-shaped corner pores), and it is probable that the transition from this genus to *Favosites* occurred independently in more than one lineage (see *Discussion* under *Paleofavosites*, p. 78).

Most septal spines in *Paleofavosites subelongus* appear to be composed of bundles of subparallel fibers, rather than being truly trabecular in form (see *Microstructure* under *P. subelongus*, p. 83). This appearance supports the observations of Schouppé and Oekentorp (1974, p. 167) on favositid septal form, and is not consistent with Sokolov's (1955, p. 28) and Hill's (1981, p. F448) idea that tabulatan septal spines are fine trabeculae.

Genus **PALEOFAVOSITES** Twenhofel, 1914

Calamopora Goldfuss, 1829, p. 77.
Paleofavosites Twenhofel, 1914, p. 24; 1928, p. 125; Poulsen, 1941, p. 20; Stearn, 1956, pp. 59, 60; Hill, 1959, p. 11; Flower, 1961, pp. 71–73; Scrutton, 1975, pp. 29, 30; Oekentorp, 1976, p. 165; Powell and Scrutton, 1978, pp. 312, 313; Laub, 1979, pp. 259–263; Hill, 1981, pp. F546, F547; Scrutton, 1985, p. 34.
Multisolenia Fritz, 1937, p. 231; Sokolov, 1950b, pp. 221, 222; 1951b, p. 50; Hill and Stumm, 1956, p. F464; Stearn, 1956, p. 65; Klaamann, 1964, p. 42; Stel, 1975, p. 61.
Palaeofavosites Twenhofel, 1914. Lang *et al.*, 1940, p. 94; Sokolov, 1950b, p. 216; 1951a, pp. 30, 31; 1951b, p. 12; Hill and Stumm, 1956, p. F461; Nelson, 1963, p. 51; Sokolov and Tesakov, 1963, pp. 39, 40; Klaamann, 1964, p. 5; Stasinska, 1967, p. 66; Oekentorp, 1971, pp. 158, 159; Hall, 1975, p. 86; Stel, 1975, p. 41.
Mesofavosites Sokolov, 1951b, pp. 59–61; Klaamann, 1964, p. 45; Stasinska, 1967, p. 76; Stel, 1975, p. 65.
Mesosolenia Mironova, 1960, p. 95.
Priscosolenia Sokolov, 1962, p. 58; Klaamann, 1964, p. 40; Stasinska, 1967, p. 73; Stel, 1975, p. 55.
Sparsisolenia Stasinska, 1967, p. 74.

Type species.—By original designation: *Favosites aspera* d'Orbigny (1850, p. 49); Aymestry Limestone (lower Upper Silurian, Ludlow), Leinthall Earls, Welsh Borderland, U.K. (Powell and Scrutton, 1978, p. 313).

Diagnosis.—Favositinae with contiguous polygonal corallites. Corner pores are characteristic; may be simple or take the form of solenia; a simple pore generally connects two corallites, may very rarely connect three corallites at a triple junction. Mid-wall pores may be present. Septa may be absent, or represented by variably developed spines arranged in vertical rows. Tabulae usually complete.

Discussion.—Twenhofel (1914, p. 24) based his original definition of *Paleofavosites* on material from Anticosti Island, Québec. He stated that *Favosites aspera* should be the type species because he thought at that time that *Paleofavosites prolificus* (Billings) and *Paleofavosites capax* (Billings) from Anticosti Island were junior synonyms of that species. Although Twenhofel (1928, p. 125) later changed this view, stating that *P. prolificus* should be the type species, *Paleofavosites asper* has been accepted as the type by all subsequent workers. This sequence of events is fortunate, since the holotype of *P. prolificus* is now known to be lost (Bolton, written commun., 1991); the lack of a type for such an important taxon could have caused considerable confusion.

Our concept of *Paleofavosites* follows the broad approach to this genus advocated by Stel and Oekentorp (1976, pp. 163–173) and Powell and Scrutton (1978, pp. 307, 308, 310, 312, 313). Like those authors, we consider genera possessing solenia (funnel-shaped corner pores) to be junior synonyms of *Paleofavosites*. These genera include *Multisolenia, Mesosolenia, Priscosolenia,* and *Sparsisolenia.* Stel and Oekentorp (1976, p. 173) suggested that, although *Multisolenia* and similar taxa are clearly congeneric with *Paleofavosites,* their solenid habit warrants placement in a distinct subgenus. Such a separation may be deemed reasonable in the future, but at present relationships among the different forms are too poorly understood for it to have any validity. The proposal by Stel and Oekentorp (1976, p. 173) that such a subgenus be named *Paleofavosites* (*Desmidopora*) should not be followed, as it was based on the incorrect interpretation of *Desmidopora* Nicholson as a subjective synonym of *Multisolenia. Desmidopora* is now considered to be a chaetetid (Stel and Oekentorp, 1980, pp. 407, 408; Hill, 1981, p. F515) or a sclerosponge (Scrutton, 1987, p. 488).

Powell and Scrutton (1978, pp. 307, 310) suggested that *Mesofavosites* should be considered a junior synonym of *Paleofavosites. Mesofavosites* was initially distinguished from *Paleofavosites* because it possesses both corner and mid-wall pores. As Powell and Scrutton noted, however, both forms of pore occur in the type species of *Paleofavosites,* and therefore both are characteristic of that genus. Corals having both corner and mid-wall pores are intermediate in evolutionary and stratigraphic position between *Paleofavosites* and *Favosites,* but it is possible that the transition in pore character occurred independently in more than one lineage at about the same time (Stearn, 1956, pp. 59, 60; see *Paleofavosites subelongus,* p. 40; *Discussion* under *Paleofavosites* sp. cf. *P. subelongus,* p. 91, and under *Paleofavosites adaensis,* p. 94). If such parallel evolution can be clearly demonstrated by future work, then it will be necessary either to synonymize *Paleofavosites* with *Favosites* or to define a new genus or genera based on characters other than pore position.

Our concept of *Paleofavosites* includes one character that was not accepted by some previous authors. Oekentorp and Schouppé (1969, p. 89) and Hill (1981, p. F547) stated that each corner pore opens into two corallites only. The material of *P. subelongus* that we examined includes one specimen that possesses an unequivocal three-way corner pore occurring at a triple wall junction (USNM 485877; Pl. 17, fig. 2), and other less well-preserved examples that may represent the same type of structure.

Paleofavosites subelongus (Savage, 1913)

Plate 13, figures 1–11; Plate 14, figures 1–11;
Plate 15, figures 1–12; Plate 16, figures 1–13;
Plate 17, figures 1–7

Favosites subelongus Savage, 1913, p. 64, pl. 3, figs. 9, 10; 1917, p. 114, pl. 5, figs. 9, 10.

Calapoecia favositoidea Savage, 1913, pp. 64, 65, pl. 3, figs. 1–3; 1917, p. 115, pl. 5, figs. 1–3.

[*cf.*] *Palaeofavosites forbesiformis* Sokolov, 1951b, pp. 28, 29, pl. 8, figs. 1, 2; Stasinska, 1967, pp. 68, 69, pl. 16, figs. 1a, 1b, table 4.

[*cf.*] *Palaeofavosites prolificus* (Billings, 1865). Nelson, 1963, p. 52, pl. 7, fig. 5.

[?] *Paleofavosites* sp. cf. *P. forbesiformis* Sokolov, 1951b. Bolton, 1981a, pl. 2, figs. 3, 4, pl. 3, figs. 9, 10.

Paleofavosites subelongus (Savage, 1913). Elias and Young, 1992, figs. 3a, 3b; Young and Elias, 1993, pl. 1, figs. 1–4, 11–16.

Diagnosis.—*Paleofavosites* with corallites of variable size; average adult corallite dimensions commonly 1.0–3.2 mm. Corallites usually have three to eight or nine sides. Walls straight, slightly wavy, or broadly curved in transverse section. Corner pores common, mid-wall pores extremely rare. Septa rod-like or thorn-like; of variable length, may be absent. Tabulae thin, flat or wavy, slightly concave or convex.

Description of coralla.—Coralla have low and high bulbous (Pl. 14, fig. 10), low and high domical (Pl. 16, fig. 5), and low columnar growth forms (Table 14). Size range is 14–77 mm wide and 9–68 mm high.

In transverse section, corallites are polygons of regular or irregular shape. Average corallite dimensions are extremely variable, 0.25–3.50 mm; average dimensions of adult corallites are commonly 1.0–3.2 mm (Table 19). Mean corallite areas on transverse sections are about 1–6 mm^2 (Table 19). Corallites usually have three to eight or nine sides, rarely up to 10 or 11 sides (Table 19). Distribution of corallite shapes is variable; where corallite sizes are regular, most corallites have five to seven sides (Pl. 15, fig. 7), but where the corallite size range is large, adult corallites with seven to nine sides are surrounded by small corallites with three or four sides (Pl. 15, figs. 11, 12, Pl. 16, fig. 1; see *Intraspecific variation,* below). In longitudinal section, corallites near the colony axis are straight; those occurring laterally are curved away from the axis (Pl. 14, fig. 10, Pl. 16, figs. 5, 12).

Corallite walls are usually straight or slightly wavy in transverse section (Pl. 13, figs. 1, 3). Walls may be broadly curved or bowed in some places (Pl. 13, fig. 1, Pl. 17, fig. 1). Wall thickness is commonly 0.05–0.20 mm (Table 19), and may vary cyclomorphically. The wall may appear to undulate between offset septa (Pl. 14, fig. 5, Pl. 16, fig. 7). In longitudinal section, walls are straight or wavy (Pl. 13, fig. 9, Pl. 14, fig. 3). Corner pores are common and irregularly distributed. Most corner pores are simple, with diameters com-

Table 19.—Biometric data for favositids from the east-central United States. *ACD* = average corallite dimensions (*all* corallites and those having 6+ sides), *CoA* = corallite area, *Pol* = polygonality (number of sides), *WT* = wall thickness, *LS* = length of septa, *PoD* = pore diameter (corner pores only), *Ta5* = number of tabulae in 5 mm, *Se5* = number of septa in 5 mm, *TC* = thickness of cycles; s.d. = standard deviation, c.v. = coefficient of variation.

species	*parameters*									
data	*ACD (all)*	*ACD (6+)*	*CoA*	*Pol*	*WT*	*LS*	*PoD*	*Ta5*	*Se5*	*TC*
Paleofavosites subelongus										
mean	1.62 mm	2.07 mm	2.72 mm^2	5.6	0.123 mm	21%	0.135 mm	4.5	19.8	13.5 mm
range of colony means	0.81–2.49 mm	1.11–2.99 mm	0.88–6.25 mm^2	4.9–6.1	0.050–0.210 mm	0–48%	0.095–0.205 mm	2.4–10.9	15.5–27.5	13.0–14.0 mm
s.d. of colony means	0.38 mm	0.46 mm	1.14 mm^2	0.3	0.038 mm	10%	0.025 mm	1.4	4.8	0.7 mm
c.v. of colony means	23.5	22.2	41.9	5.4	30.9	47.6	18.3	31.7	24.2	5.2
minimum	0.25 mm	0.85 mm	—	3	0.025 mm	—	0.050 mm	1	12	—
maximum	3.50 mm	3.50 mm	—	11	0.450 mm	—	0.300 mm	12	30	—
mean intracolony c.v.	35.5	13.2	—	27.0	20.0	—	20.2	20.1	10.0	—
no. of coralla studied	102	102	82	102	58	47	32	79	5	2
Paleofavosites sp. cf. *P. subelongus*										
mean	1.65 mm	2.06 mm	2.90 mm^2	5.8	—	—	0.150 mm	4.9	—	—
range of colony means	1.19–1.98 mm	1.68–2.46 mm	2.13–3.92 mm^2	5.0–6.1	—	—	—	4.0–5.8	—	—
s.d. of colony means	0.27 mm	0.28 mm	0.81 mm^2	0.4	—	—	—	1.3	—	—
c.v. of colony means	16.4	13.6	27.9	6.9	—	—	—	26.5	—	—
minimum	0.38 mm	1.25 mm	—	3	—	—	0.100 mm	2	—	—
maximum	3.00 mm	3.00 mm	—	12	—	—	0.200 mm	14	—	—
mean intracolony c.v.	33.6	11.1	—	28.9	—	—	28.0	18.5	—	—
no. of coralla studied	7	7	5	7	—	—	1	2	—	—
Paleofavosites adaensis										
mean	3.55 mm	4.04 mm	11.30 mm^2	6.0	0.049 mm	0	0.205 mm	4.7	—	—
range of colony means	3.05–4.11 mm	3.32–5.28 mm	7.69–17.40 mm^2	5.8–6.2	0.032–0.070 mm	0–0	—	2.2–8.1	—	—
s.d. of colony means	0.45 mm	0.70 mm	4.03 mm^2	0.1	0.016 mm	0	—	2.4	—	—
c.v. of colony means	12.7	17.3	35.6	1.7	32.7	0	—	51.1	—	—
minimum	0.58 mm	2.25 mm	—	3	0.025 mm	—	0.100 mm	1	—	—
maximum	5.82 mm	5.82 mm	—	10	0.100 mm	—	0.325 mm	10	—	—
mean intracolony c.v.	28.0	10.5	—	20.5	26.0	—	31.0	22.6	—	—
no. of coralla studied	7	7	6	7	4	4	1	6	—	—
Paleofavosites sp. cf. *P. ivanovi*										
mean	2.55 mm	3.30 mm	5.67 mm^2	5.8	0.069 mm	4%	0.121 mm	1.8	—	—
range of colony means	2.49–2.61 mm	3.26–3.35 mm	5.19–6.15 mm^2	5.7–5.9	—	—	—	—	—	—
s.d. of colony means	0.08 mm	0.06 mm	0.68 mm^2	0.1	—	—	—	—	—	—
c.v. of colony means	3.1	1.8	12.0	1.7	—	—	—	—	—	—
minimum	0.50 mm	2.58 mm	—	3	0.050 mm	—	0.075 mm	1	—	—
maximum	4.25 mm	4.25 mm	—	10	0.100 mm	—	0.175 mm	2	—	—
mean intracolony c.v.	34.0	10.7	—	28.4	23.2	—	27.3	10.7	—	—
no. of coralla studied	2	2	2	2	1	1	1	1	—	—
Paleofavosites sp. A										
mean	2.05 mm	2.34 mm	3.39 mm^2	5.9	0.086 mm	0%	—	4.1	—	18.5 mm
range of colony means	1.88–2.21 mm	2.20–2.47 mm	2.84–4.00 mm^2	5.6–6.3	—	—	—	3.0–6.2	—	—
s.d. of colony means	0.13 mm	0.11 mm	0.48 mm^2	0.3	—	—	—	1.3	—	—
c.v. of colony means	6.3	4.7	14.2	5.1	—	—	—	31.7	—	—
minimum	0.55 mm	1.82 mm	—	3	0.050 mm	—	—	2	—	—
maximum	2.82 mm	2.82 mm	—	9	0.125 mm	—	—	8	—	—
mean intracolony c.v.	26.4	9.8	—	22.2	32.6	—	—	27.6	—	—
no. of coralla studied	6	6	4	6	1	1	—	5	—	1

monly 0.08–0.25 mm (Table 19). The end of a wall adjacent to a pore is usually square and bulges slightly (Pl. 14, fig. 4, Pl. 16, fig. 11). Corner pores commonly have thin pore plates that are straight or are strongly curved into the lumina of corallites. Three-way corner pores, each connecting three adjacent corallites, occur rarely (Pl. 17, fig. 2). Where corallites are smaller, corner pores may take the form of solenia (funnel-shaped pores; Pl. 13, fig. 4, lower left side). In longitudinal section, solenia occur in regular rows. Mid-wall pores with diameters of about 0.10 mm occur rarely in a few coralla (Pl. 16, fig. 10; see *Paleofavosites subelongus,* p. 40).

In transverse section, septa are absent (Pl. 13, fig. 5, Pl. 15, fig. 7) to thick and thorn-like (Pl. 13, fig. 10), rod-like with square tips (Pl. 14, fig. 9, Pl. 15, fig. 11), or long and slender (Pl. 14, fig. 5). Septal length is variable, commonly up to 25% of corallite radius, but may be 50% of radius in newly initiated corallites (Table 19). In coralla with smaller than average corallites, septa are commonly rare or absent (Pl. 13, fig. 5). Where septa are well developed, a corallite contains as many septa as its size will allow; up to 37 septa in transverse section. In adjacent corallites, septa on opposite sides of a wall may be either opposed or alternating. In longitudinal section, septa may be straight and upwardly directed or horizontal, or may be downcurved adaxially; angles of septa in a single corallum may vary significantly in longitudinal section (Pl. 13, fig. 7, Pl. 16, fig. 6). Septal spines occur in rows that may change in number as septa are inserted with height in a corallite (Pl. 15, fig. 9); vertical spacing is 12–30 septal spines per 5 mm (Table 19). Septa are variably developed between coralla and between areas of a single corallum (Pl. 14, fig. 11, Pl. 15, fig. 2); in areas where tabulae are closely spaced cyclomorphically, septa may be very thick and abundant.

Tabulae are moderately thin. They are flat, wavy, or slightly concave or convex, and may curve upward laterally to meet the corallite wall (Pl. 13, fig. 2, Pl. 15, fig. 2). They are usually complete, very rarely incomplete (Pl. 16, fig. 12). The shapes of tabulae in transverse section indicate that they are often crenulate, with the arches of crenulations occurring near the corners of corallites (Pl. 14, fig. 1). In longitudinal section, tabulae are widely spaced, averaging about 4 in 5 mm (Table 19). In some coralla, tabular spacing varies cyclomorphically, with pairs of closely spaced and widely spaced bands of tabulae averaging 13.5 mm in thickness (Table 19; Pl. 14, fig. 10, Pl. 16, fig. 12). Tabulae are occasionally quite irregular in form, having lobe-like axial depressions or subcircular cavities axially (Pl. 14, figs. 2, 7). Tabulae hang from septal spines in some places (Pl. 14, fig. 6). They are often thickened where they connect with the corallite wall.

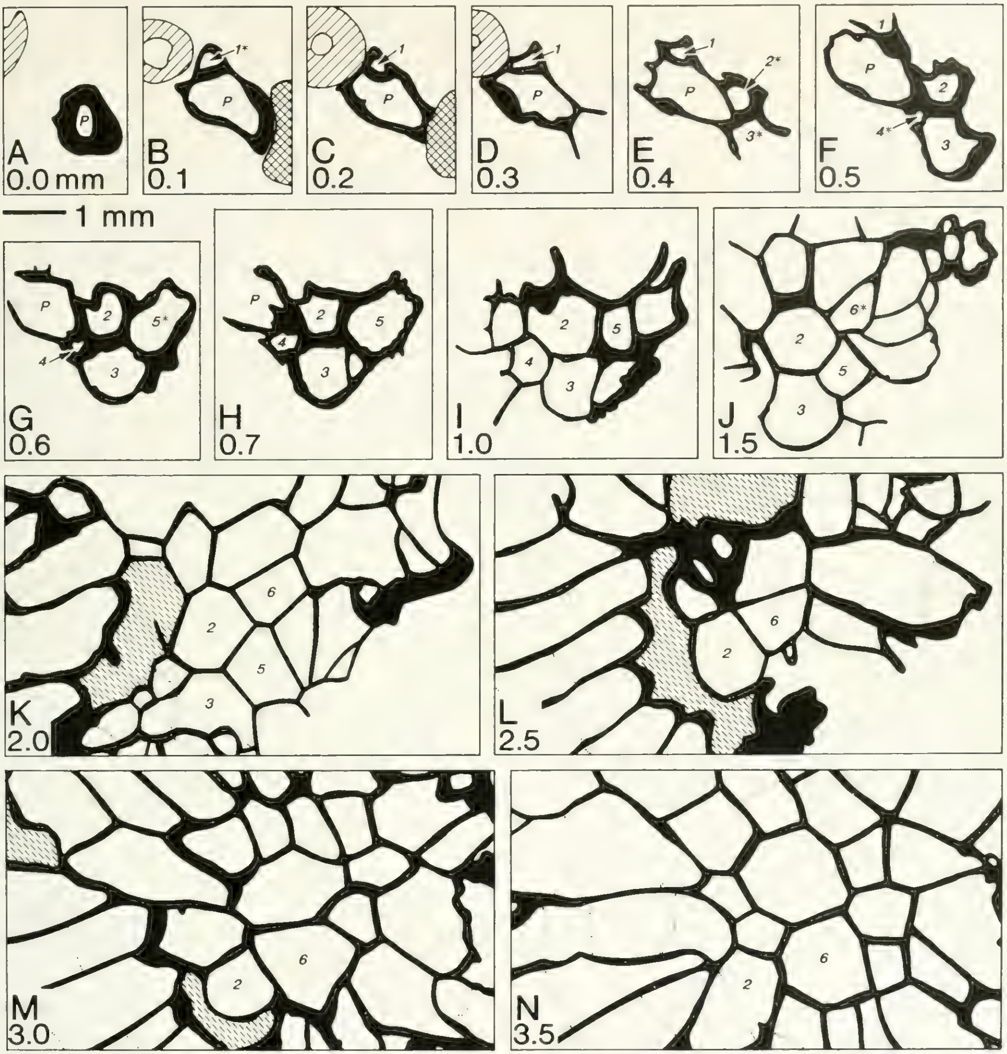
Astogeny and corallite increase.—Descriptions are based principally on four serial-sectioned coralla (USNM 459074, 459079, 459086, 485865) and one serial-sliced corallum (USNM 459080). Other specimens are used for comparison.

A full sequence of basal growth can be reconstructed in one serial-sectioned corallum (USNM 459086; Text-fig. 22). Initially, the protocorallite has a subovate lumen, an irregular external outline, and dimensions of 0.85 by 0.60 mm; it is thick-walled, apparently aseptate (Text-fig. 22A). The protocorallite is probably based on an algal grain. At about 0.1 mm above its base the protocorallite was joined by a small hysterocorallite; rapid offsetting followed, and by 0.5 mm above its base the corallum consisted of five corallites (Text-fig. 22B–F). Rare septa occur in the first 0.5 mm of the protocorallite; these are short, thick, and node-like. The protocorallite grew to a height of 0.7–0.8 mm prior to death. In its last complete section the protocorallite is oblique to the other individuals and has dimensions of 1.55 by 0.95 mm.

Several phases of lateral expansion and contraction occurred before the corallum was able to establish a spreading cerioid "base" at about 3.5 mm above the absolute base of the protocorallite (Text-fig. 22G–N). Through this growth phase, corallites have irregular shapes and sizes; the corallum axis is small, and divergence is often marked. Corallites positioned at the margins were commonly short-lived. At 3.5 mm above the absolute base, the larger corallites have average dimensions of about 1.3–1.7 mm, well within the range for adult corallites of this species. The corallite walls are thick, and septal spines are present. The later development of this corallum is typical of large-corallite variants of this species (see *Intraspecific variation,* below).

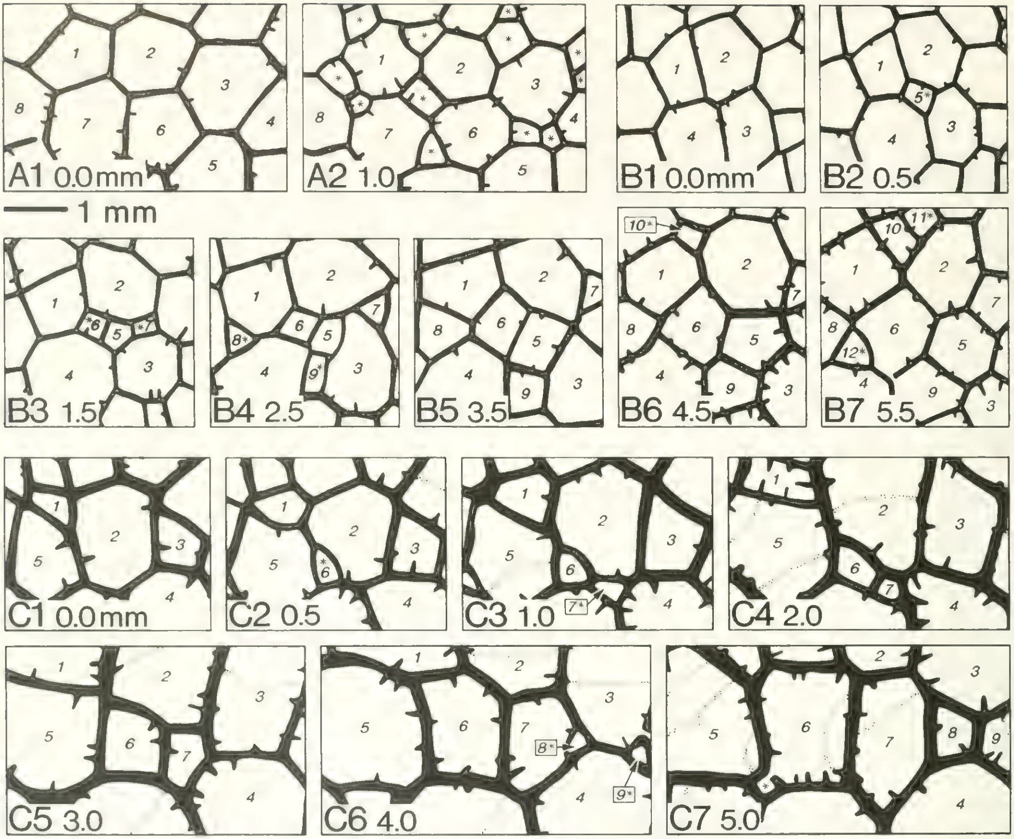
Coralla of this species are generally similar in basal character, but some significant differences appeared quite early in growth. At or near the bases of coralla, corallites tend to be small, with average dimensions commonly 0.75–1.80 mm. They are aseptate or weakly septate, of regular or somewhat variable size, and are commonly relatively thick-walled (Pl. 16, fig. 5). In coralla that went on to develop large corallites, corallum bases are broadly divergent; this is associated with a rapid increase in average corallite dimensions during the early growth stages (Pl. 16, fig. 5). In coralla of the small-corallite variant (see *Intraspecific variation,* below), bases are much less divergent, and corallites near the absolute base already have average corallite dimensions close to those seen in later stages of growth (Pl. 14, fig. 10).

During subsequent growth, corallites in the corallum axis continued to expand slowly, with corallite contraction occurring at rare intervals in some specimens.



Text-figure 22.—A–N, Serial transverse sections illustrating basal astogeny in a corallum of *Paleofavosites subelongus;* USNM 459086, Section-interval 16-1 (Clinton Spring) (see also Pl. 14, figs. 1–3). Corallite walls are solid, tabulae are stippled, septa are not shown; a probable algal grain is cross-hachured, a crinoid columnal is solid-hachured, sediment surrounded by the corallum is dash-hachured; scale bar is shown. Section A (0.0 mm) represents the absolute base of the corallum, heights in mm for B–N are above that datum; *P* is the protocorallite, numbers in italics represent individual hysterocorallites; an asterisk indicates the first appearance of a particular hysterocorallite.

Variability of corallite dimensions on transverse sections is commonly quite different between sections taken from different heights within a single corallum (see *Intraspecific variation,* below). Walls and septa show normal characters of development quite low in a corallum, but both tended to change through growth. Well defined cyclomorphic variation is rare (see *Description of coralla,* above); where it is present, thick-



Text-figure 23.—Serial transverse sections illustrating corallite increase in *Paleofavosites subelongus*. **A1, A2**, Burst of offsetting in a corallum where mature corallites are of regular size; USNM 459074, Section-interval 15-1 (Calumet) (see also Pl. 14, figs. 9–11). **B1-B7**, Corallite increase in a corallum having small corallites of relatively regular size; USNM 485865, Section-interval 14-1 (Higginbotham Farm). **C1-C7**, Corallite increase in a corallum having relatively large, dimetric corallites; USNM 459079, Section-interval 14-1 (Higginbotham Farm) (see also Pl. 16, figs. 1–6). Corallite walls and septa are solid, tabulae are stippled; scale bar is shown. Heights in mm are above an arbitrary datum within the mature, axial part of each corallum; numbers in italics represent individual corallites; an asterisk indicates the first appearance of a particular corallite.

ening of walls and increased density and length of septa do not always occur in conjunction with closer spacing of tabulae. Single corallites commonly extend through most or all of the height of a corallum. Skeletal elements occurring at the upper surfaces of coralla are not obviously different from those occurring below.

Corallite increase is intracalicular and peripheral (= lateral); each new corallite was produced through the development of a wall that closed off a corner or a side of the parent corallite (Text-fig. 23; Pl. 14, fig. 1, Pl. 15, fig. 11). Each offset is connected to its parent by one or two pores at or immediately above its base. New offsets have three or four sides, depending on whether the site of increase was in a corner or along a wall (Pl. 16, figs. 3, 4); sides were added as corallites grew (Young and Elias, 1993). Four-sided offsets are most common where mature corallites are more regular in size (Pl. 15, figs. 8, 12), whereas three-sided offsets predominate in coralla showing more pronounced dimetrism (Text-fig. 23; Pl. 15, fig. 11). Parent corallites were usually relatively large, typically having five to eight sides prior to offsetting. Although in many cases the parent corallite cannot be distinguished due to plane of sectioning, it seems that new offsets did not generally give rise to other offsets except during regeneration following partial mortality of the colony surface.

New corallites typically expanded quite slowly (Text-fig. 23; see *Intraspecific variation,* below). Expansion rates were highest in coralla having large adult corallites, and were significantly lower where adult corallites were smaller (Young and Elias, 1993). Each new corallite expanded into space previously occupied by the adjacent individuals (Text-fig. 23B1–B7, C1–C7). New corallites may be aseptate (Pl. 16, fig. 3) or may have very long septa (Pl. 16, fig. 11, lower right). The walls of three-sided corallites are commonly bowed outward (Pl. 14, fig. 8).

In most coralla there are obvious differences between the axis (area of vertical and subvertical growth) and the margins (areas of more lateral growth); in some coralla there is a clear distinction between these regions (Pl. 16, fig. 5). Corallites are usually straight in the axis, but they tend to be curved outward in the margins. Tabulae are more broadly spaced in the axis than in the margins; this is more marked in domical coralla than in bulbous ones. Cyclomorphic bands extend across the entire corallum. Offsetting was often concentrated in the axis, and particularly at the transition between the axis and margins. The relative width of the axis and margins reflects corallum growth patterns and the shape of the growth surface. A relatively broad axis is associated with a tall corallum having short growth surfaces. Such coralla tend to have developed where basal divergence was restricted, and where adult corallites were small. Relatively narrow axes and wider margins occur in coralla with more spreading growth forms, long growth surfaces, more basal divergence, and large corallites (see *Intraspecific variation,* below).

Sediment inclusions representing partial mortality of the colony surface occur in many specimens (Pl. 16, fig. 12). Such inclusions can occur in both marginal and axial areas. Above these inclusions, variable patterns of growth are observed. In some cases, new subvertical corallites that are slightly smaller than the previous adult individuals were initiated across the surface of a holothecal layer (Pl. 15, fig. 6). Such corallites are commonly irregular in outline and may be predominantly five-sided (Pl. 16, fig. 9); they developed normal adult size and appearance during subsequent growth. In other examples, corallites occurring lateral to an inclusion spread subhorizontally across the inclusion, giving rise to offsets before resuming subvertical growth (Pl. 16, fig. 12).

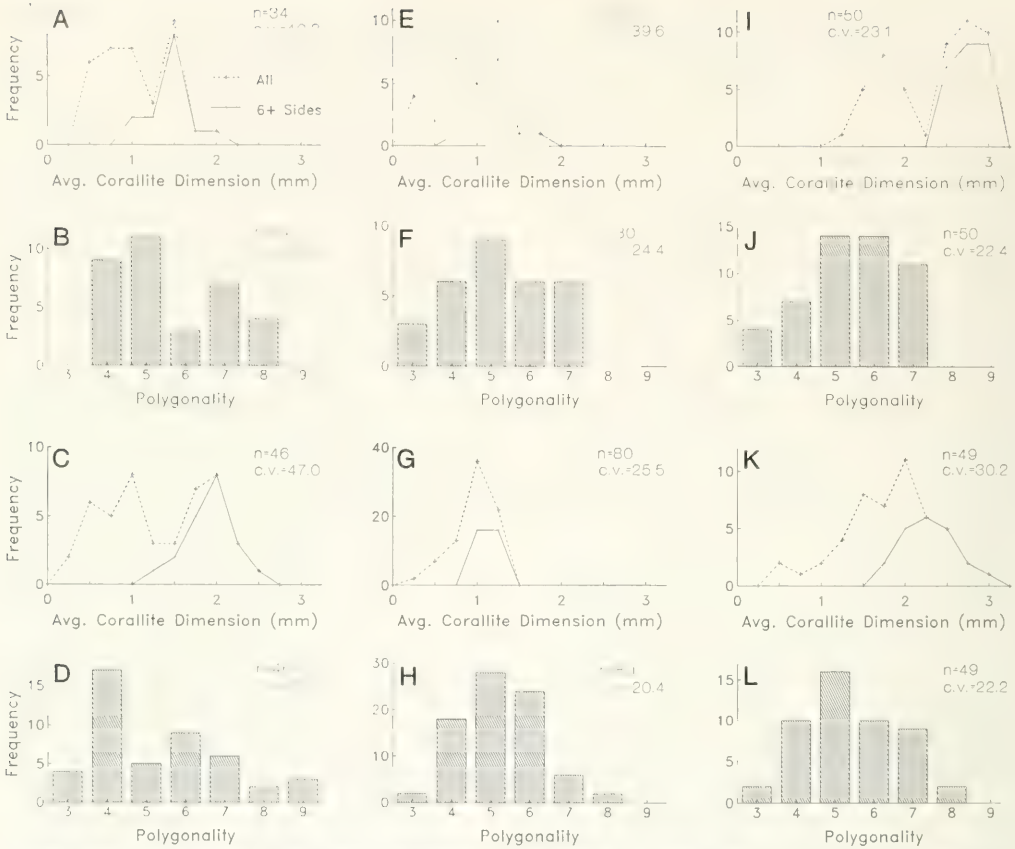
Microstructure. — The wall between any pair of corallites is composed of three layers: a "dark" median line (see Schouppé and Oekentorp, 1974, fig. 6) bounded on either side by a radially fibrous layer. The median line has a lamellar appearance. It has definite lateral boundaries and is usually slender, but its thickness varies considerably between coralla depending on preservation (Pl. 14, figs. 3, 7, Pl. 15, figs. 1, 2, Pl. 16, figs. 3, 4, 10); it can be darker or paler than the rest of the wall. The median line can maintain a consistent thickness between cyclomorphically thickened and unthickened parts of a corallum. The fibrous layers of the wall are usually buff-colored and consist of fibers that are perpendicular to the wall in transverse section, and directed upward laterally from the median line at an angle from the horizontal of about 30–60° in longitudinal section (Pl. 15, fig. 4).

Septal spines are usually embedded deep in the fibrous wall, and the fixed part of each septum follows the prevailing trend of wall fibers (Pl. 15, fig. 4). They are rarely fixed in the median line. Septa are usually denser or darker in color than the wall fibers. Most septal spines appear to be composed of bundles of subparallel fibers, rather than being truly trabecular in form. The adaxial parts of septal fibers may be straight, following the trend of the septal base (Pl. 13, fig. 7), or they may be upcurved or downcurved (Pl. 16, fig. 6).

Microstructure of tabulae is indistinct. Tabulae are embedded in the outermost margin of the fibrous wall, and are generally similar in color to that wall.

Intraspecific variation. — There is great variability among the coralla described above. This involves a number of characters, including corallite size, polygonality, wall thickness, septal development, and spacing of tabulae.

Frequency distributions of corallite size from individual transverse sections are extremely variable (Text-fig. 24A, C, E, G, I, K). Corallites added sides in a more or less regular manner as they grew, and frequency distributions of corallite size and polygonality in transverse sections tend to mimic one another (Text-fig. 24), although there are exceptions. There is no set frequency pattern of corallite size or polygonality for any one locality or corallite size range (Text-fig. 24), and distributions may vary significantly between transverse sections from different heights within a single corallum (Text-fig. 24E–H). Frequency distributions seem to have depended on periodic offsetting, and on the slow rate of corallite expansion (see *Astogeny and corallite increase,* above; *Paleofavosites subelongus,* pp. 38, 39). The modes on bimodal or polymodal distributions represent different periods of offsetting. For coralla from all localities, those corallites with six and more sides show virtually normal size distributions (Text-fig. 24A, C, E, G, I, K).



Text-figure 24.—Frequency distributions of average corallite dimension (all corallites and those with six and more sides) and polygonality for selected coralla of *Paleofavosites subelongus*. **A, B**, USNM 485822, Section-interval 31-1 (Thebes North). **C, D**, USNM 485835, Section-interval 15-1 (Calumet). **E–H**, USNM 459082, Section-interval 14-1 (Higginbotham Farm); E and F near corallum base, G and H higher in corallum. **I, J**, USNM 485855, Section-interval 14-1 (Higginbotham Farm). **K, L**, USNM 485900, Section-interval 32-1z (Thomson East). Each pair of graphs represents the same single transverse section; n = number of corallites (all), c.v. = coefficient of variation for all corallites.

Although corallite size frequency distributions are variable, there is a strong linear relationship between the average dimension of all corallites and the average dimension of corallites with six and more sides in transverse sections of this species (Text-fig. 25A). This relationship remains roughly constant with changes in corallite size. Also, the variability of corallite size within coralla does not change with changes in mean size, and there is no clear correlation within coralla between variability in size of all corallites and of those having six and more sides.

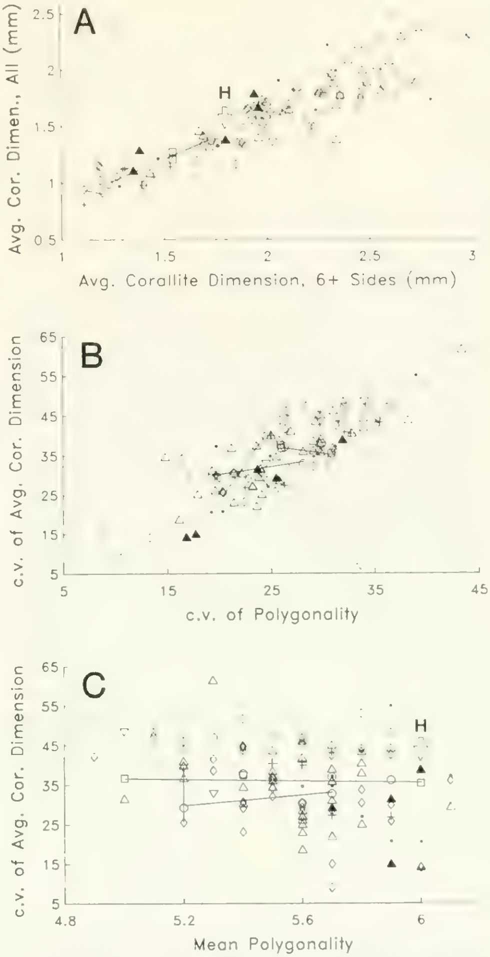
There are some differences in the range of corallite size between stratigraphic intervals for which large collections are available (Text-fig. 25A), and this variation is correlated with colony growth form. Coralla having domical forms with flat bases tend to have the largest corallites, whereas those having bulbous or columnar forms with expanding bases tend to have smaller corallites (see *Astogeny and corallite increase*, above). Coralla with the largest average corallite dimensions occur in Section-interval 32-1z (Thomson East) (mean ACD (6+) = 2.28 mm), where coralla are predominantly of high and low domical form (Table 14; Text-fig. 10). Coralla from Section-intervals 14-1 (Higginbotham

Farm) and 15-1 (Calumet) have somewhat smaller corallites (mean ACD (6+) = 2.09 mm and 1.99 mm, respectively), and coralla from these intervals are of mixed high and low domical and bulbous form (Table 14; Text-fig. 10). Coralla with much smaller corallites were collected from Section-interval 31-1 (Thebes North) (mean ACD (6+) = 1.35 mm; Text-fig. 25A). Unfortunately, data are insufficient to determine whether the coralla are predominantly tall in this collection, but it is noteworthy that the tallest forms of *Propora thebesensis* occur in the same interval.

There is a correlation between the variabilities of average corallite dimension and polygonality (Text-fig. 25B). Transverse sections having highly variable corallite sizes are also highly variable in polygonality. The variability of average corallite dimension is also correlated with the mean of polygonality (Text-fig. 25C). Where the variability of corallite size is great, the mean polygonality is often well below 6.0. This suggests that an increase in the number of three- and four-sided corallites on a surface, due to offsetting, was not quite matched by an increase in the number of corallites having seven or more sides. Most of the range of mean polygonality can occur within single coralla. Each large collection shows a considerable range of polygonality, and a range of variability in polygonality and average corallite dimension (Text-fig. 25B, C).

Comparisons between coralla in this entire collection show that a relationship exists between corallite size and the degree of development and thickening of skeletal characters. A graph of mean wall thickness *versus* average corallite dimension of adult corallites illustrates a positive correlation between these characters (Text-fig. 26A). Most localities show a broad spread of points, but there are differences; walls are generally thicker for a given corallite size in Section-interval 14-1 than in Section-interval 32-1z. Septal length also shows a positive correlation with average corallite dimension of adult corallites (Text-fig. 26B). Relatively long septa tend to occur only where adult corallites are large, but septa may also be absent in such circumstances. The diameter of corner pores has a linear relationship with average corallite dimension of mature corallites (Text-fig. 26C); data for pore diameter are not as extensive as for wall thickness or for length of septa, but there seem to be few differences between localities for this character. Wall thickness, length of septa, and pore diameter all show a positive correlation with one another, as well as being related to corallite size.

Vertical spacing of tabulae does not show any clear relationship to corallite size, but does vary with locality (Text-fig. 26D). In Section-intervals 14-1 and 15-1, spacing of tabulae is generally close but variable,

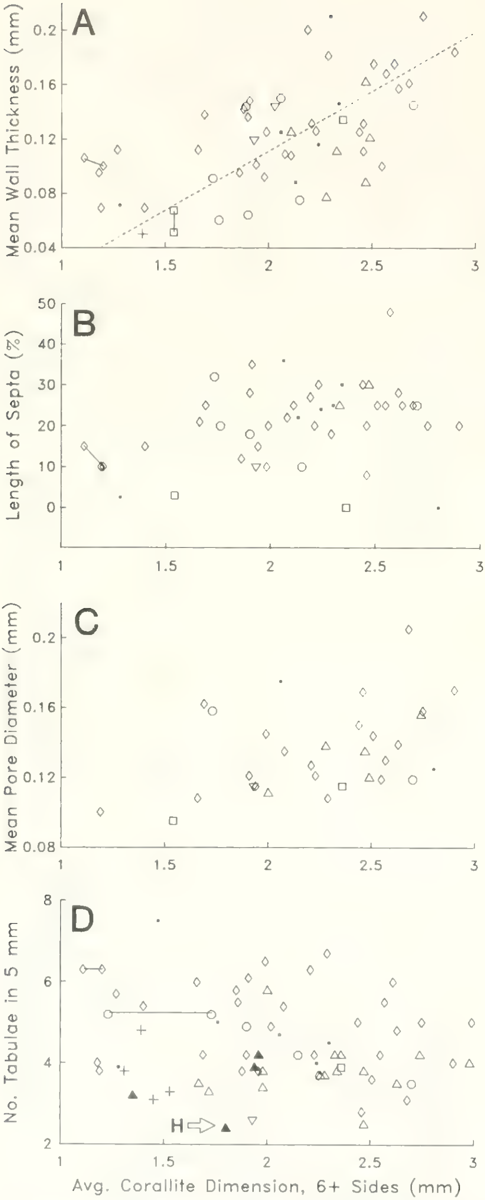


Text-figure 25.—Intercorallum variation in morphologic characters of *Paleofavosites subelongus*, Part 1. **A**, Relationship between average corallite dimension of all corallites and of those having six and more sides, for transverse sections from 102 coralla. **B**, Relationship between coefficient of variation (c.v.) of average corallite dimension (all corallites) and of polygonality for transverse sections from 102 coralla. **C**, Relationship between c.v. of average corallite dimension (all corallites) and mean polygonality for transverse sections from 102 coralla. Each data point represents a single thin section; solid lines connect sections from different parts of a single corallum; H = UI X-878a (holotype). Arbitrary dashed lines in A and B were used to derive proportions shown in part of Table 13. Symbols for Section and Section-intervals: □ 23-2 and 23-3 (Lawrence Quarry); + 31-1 (Thebes North); ▲ 5 km south of Clarksville, Missouri; ▽ 16-1 (Clinton Spring); ◇ 14-1 (Higginbotham Farm); ○ 15-1 (Calumet); △ 32-1z (Thomson East); ■ all other Section-intervals.

whereas it is broader in Section-intervals 31-1 and 32-1z, and at 5 km south of Clarksville (Table 12; Text-fig. 26D). There is no obvious general relationship between spacing of tabulae and colony growth form. Spacing of tabulae tends to be closer in marginal parts of the corallum than in the axis, and can also vary between the base and top of a corallum. This makes it difficult to compare corallum means that are in some cases based on incomplete specimens.

Discussion.—The high degree of variability observed in the collection described above makes species discrimination somewhat difficult, since such variation in several characters would be sufficient to divide the coralla into two to four species according to commonly used approaches to favositid systematics. Nevertheless, some features, such as basal morphology and the form of septa, walls, and corner pores, are reasonably consistent among all the specimens, and certain aspects of the variability in other characters support inclusion in a single species. First, a significant portion of the intercolony variation for each character may be exhibited by individual coralla. Also, corallum means for each of these characters are continuously distributed within this collection, and may show a high degree of variability within individual stratigraphic intervals. Finally, most of these characters show a moderate to strong correlation with one another; this interconnection suggests that one basic structural design was being affected by intraspecific genetic variability and environmental factors. Observations that support this interpretation are detailed under *Intraspecific variation,* above.

Savage (1913, 1917) based *Favosites subelongus* on material collected from the Cyrene Formation near Edgewood and from the Bryant Knob Formation at Louisiana and 5 km south of Clarksville, Missouri. The original description of this species emphasized corallites of variable size with dimensions up to 1.5–2.0 mm, that have corner pores and seem to lack septa. Savage's holotype (UI X-878a; Pl. 13, figs. 8, 9) and



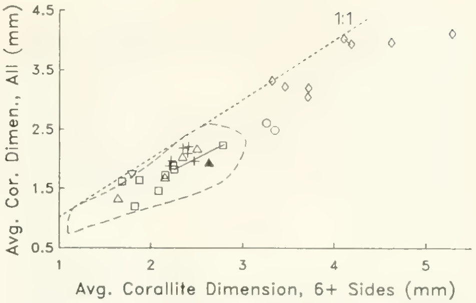
Text-figure 26.—Intercorallum variation in morphologic characters of *Paleofavosites subelongus,* Part 2. **A**, Relationship between mean wall thickness and average corallite dimension of those having six and more sides, for transverse sections from 55 coralla. **B**, Relationship between length of septa as a percentage of corallite radius and average corallite dimension of those having six and more sides, for transverse sections from 45 coralla. **C**, Relationship between mean pore diameter and average corallite dimension of those having six and more sides, for transverse sections from 31 coralla. **D**, Relationship between number of tabulae in unit 5 mm and average corallite dimension of those having six and more sides, for transverse and longitudinal sections from 67 coralla. Each data point represents a single thin section or a pair of transverse and longitudinal thin sections; solid lines connect sections from different parts of a single corallum; H = UI X-878a (holotype). Arbitrary dashed line in A was used to derive proportions shown in part of Table 13. Symbols for Section and Section-intervals are listed under Text-figure 25.

his other illustrated specimen (UI X-878b), both from 5 km south of Clarksville, are consistent with his description. Both have corallites slightly smaller than the species mean (mean ACD (6+) = 1.80 mm and 1.94 mm, respectively; compare with Table 19), short septa, thin walls, and widely spaced tabulae (Ta5 = 2.4 and 3.9, respectively). These features are consistent with those of the other material we include in *Paleofavosites subelongus,* but the holotype does not in any way represent a species "mean" for most characters.

In the same publications, Savage (1913, 1917) erected *Calapoecia favositoidea.* This species was listed as occurring at exactly the same localities as *F. subelongus,* and was described as having polygonal corallites with dimensions of 1.5–2.5 mm, in contact, and walls with spiniform ridges. Savage's diagram of a transverse section and photograph of *C. favositoidea* (Savage, 1913, pl. 3, figs. 1, 3; 1917, pl. 5, figs. 1, 3) show characters that are completely consistent with those of *Paleofavosites subelongus,* and the two species are considered to be synonyms. Savage's assignment of *C. favositoidea* to *Calapoecia* was apparently based on his interpretation of corallite walls exposed in longitudinal section as areas of small pores (see Savage, 1913, pl. 3, fig. 2; 1917, pl. 5, fig. 2). The specimen labelled as the holotype of *C. favositoidea* (UI X-771; Pl. 14, figs. 4–6) is not the same as that illustrated by Savage (1913, pl. 3, fig. 1; 1917, pl. 5, fig. 1); the original specimen is apparently lost. All identifiable specimens collected by Savage that are labelled as *C. favositoidea* (UI X-771, C-1457, C-1458b–g, and C-1465a, b) are members of *P. subelongus* (see also Pl. 13, figs. 10, 11, Pl. 15, figs. 1, 2).

Among the other described species of *Paleofavosites, P. subelongus* is most similar to *Paleofavosites* sp. cf. *P. forbesiformis* from the lower part of member 1 of the Becscie Formation on Anticosti Island, Québec (lowermost Silurian, Lower Llandovery, lowermost Rhuddanian; Melchin *et al.,* 1991, p. 1861), as illustrated by Bolton (1981a; unit referred to as member 6 of the Ellis Bay Formation therein). We examined the following specimens, collected by T. E. Bolton in 1957 and 1958: GSC 66830 (Bolton, 1981a, pl. 2, fig. 3), 66831 (Bolton, 1981a, pl. 2, fig. 4), 66839 (Bolton, 1981a, pl. 3, fig. 9), and 66840 (Bolton, 1981a, pl. 3, fig. 10).

Bolton's specimens of *Paleofavosites* sp. cf. *P. forbesiformis* are similar to *P. subelongus* for most characters, including corallite size, wall thickness, and form of pores and septa (biometric data for the Anticosti *Paleofavosites* sp. cf. *P. forbesiformis:* ACD (all) = 1.32–2.16 mm, ACD (6+) = 1.64–2.50 mm, CoA = 1.59–4.35 mm^2, Pol = 5.8–6.0, WT = 0.100–0.129 mm, LS = 4–22%, PoD = 0.114–0.130 mm, Ta5 = 5.6–6.1; compare with Table 19; see Text-fig. 27). They differ from *P. subelongus* by having wavier walls and more crenulate tabulae, and one specimen (GSC 66830) appears to have more abundant mid-wall pores than does *P. subelongus.* These species are questionably synonymized here.



Text-figure 27.—Comparison of selected species of *Paleofavosites:* relationship between average corallite dimension of all corallites and of those having six and more sides, on transverse sections. Each data point represents a single thin section; solid line connects sections from different parts of a single corallum. The short-dashed line is for a relationship of 1:1; any point along this line represents a section on which all corallites are as large as those having six and more sides. A long-dashed line surrounds the field of distribution for 102 coralla of *P. subelongus* from the east-central United States. Symbols for other species: □ *Paleofavosites* sp. cf. *P. subelongus;* east-central United States; n (number of coralla) = 7; ◇ *P. adaensis;* east-central United States; n = 7; ○ *Paleofavosites* sp. cf. *P. ivanovi;* east-central United States; n = 2; + *Paleofavosites* sp. A; east-central United States; n = 6; △ *Paleofavosites* sp. cf. *P. forbesiformis;* Becscie Formation, Anticosti Island, Québec; n = 4; ▲ *P. capax;* Gun River Formation, Anticosti Island, Québec; n = 1; ▽ *P. prolificus;* Chasm Creek Formation, northern Manitoba; n = 1.

Palaeofavosites [*sic*] *forbesiformis* was originally described and illustrated by Sokolov (1951b) from the Juuru Stage of Estonia (Rhuddanian), and was documented under the same name from erratic boulders in Poland by Stasinska (1967). Their specimens have corallites with dimensions of 0.5–2.4 mm and 0.6–2.0 mm, respectively; because they have very thin walls and lack septa, and because Stasinska's (1967, pl. 16, fig. 1a) photograph of a transverse section seems to show some mid-wall pores, they are listed with a *confer* in our synonymy.

The names *Paleofavosites prolificus* and *Paleofavosites capax,* both erected for species originally described from Anticosti Island, have been used by several authors for corals having characters similar to those of *P. subelongus.* Billings (1865, p. 429) proposed *Favosites prolificus* to include specimens from the Vauréal Formation (Hudson River Group of Billings: Upper

Ordovician, Richmondian; Petryk, 1981, fig. 4) and from higher parts of the Anticosti sequence. His description of *F. prolificus* includes corallite diameters of about 2 mm ("about 1 line" in Billings), numerous tabulae, and no identifiable septa or mid-wall pores (on hand specimens). The following year, Billings (1866, p. 6) republished the same description. On the same page, he erected *Favosites capax* to include corals from the "West end" of Anticosti Island (Vauréal Formation?) having corallites with diameters of about 4 mm ("about 2 lines" in Billings) with a few smaller individuals between them, thin and flat tabulae, and corner pores. Both of these original descriptions are sufficiently general that they could refer to several different taxa. Unfortunately, the type material of both species has been lost (Bolton, written commun., 1991), and both *P. prolificus* and *P. capax* require extensive re-assessment. This uncertain status makes comparisons difficult.

Later works dealing with corals from several formations on Anticosti Island have used the species names *prolificus* and *capax*. These include studies by Twenhofel (1914, p. 24; 1928, pp. 125–127), Bolton (1981a, pl. 1, fig. 8, pl. 9, fig. 10), and Lee and Noble (1990, pp. 257–272, figs. 1–14, tables 1, 2). None, however, has described or illustrated these species in sufficient detail to permit satisfactory comparisons. From the available information, it is probable that some of the Anticosti specimens referred to *P. prolificus* are very similar to *P. subelongus*. Also similar is a specimen of *P. capax* from the lower part of member 5 of the Ellis Bay Formation (uppermost Ordovician, Gamachian; Petryk, 1981, fig. 4), illustrated by Bolton (1981a, pl. 1, fig. 8; member 5 therein). It has short septa and crenulate tabulae, but its corallites with adult dimensions of 3.2–4.0 mm are somewhat larger than those of *P. subelongus*. Other material is quite different; specimens of *P. capax* illustrated by Bolton (1980, pl. 2.7, fig. 4) from the Ellis Bay Formation and by Bolton (1981a, pl. 9, fig. 10) from the Gun River Formation (Middle Llandovery, lower Aeronian; Barnes, 1988, fig. 2) have large corallites, thin walls that have some mid-wall pores, and very rare short septa (see *Discussion* under *Paleofavosites* sp. cf. *P. ivanovi*, p. 95, for biometric data on the Gun River specimen). Bolton's (1980, pp. 22, 25, pl. 2.7, figs. 1, 5, 6) *P. capax* from the Burmingham Member of the White Head Formation near Percé, Québec (Upper Ordovician, Ashgill, pre-Hirnantian; see Skidmore and Lespérance, 1981, p. 38; Lespérance *et al.*, 1987, fig. 4), has large corallites with adult dimensions of 3.3–4.0 mm, thin walls, and some mid-wall pores.

Corals from other parts of North America have been described as *P. prolificus* and *P. capax* by several authors. Like the Anticosti Island material, all of them require detailed re-study. Corals referred to *P. prolificus* are generally the most similar to *P. subelongus*. Stearn (1956, p. 60, pl. 4, fig. 1, pl. 10, fig. 13) described and illustrated as *P. prolificus* corals from the Stony Mountain Formation (Upper Ordovician, Richmondian; Sweet, 1979, fig. 4), Stonewall Formation (uppermost Ordovician–Rhuddanian; Sweet, 1979, p. 54, fig. 4; Johnson and Lescinsky, 1986, fig. 2), Inwood Formation (Aeronian; Johnson and Lescinsky, 1986, fig. 2), and East Arm Formation (Upper Llandovery, Telychian; Johnson and Lescinsky, 1986, fig. 2) of southern Manitoba. These are described as having corallites with uniform dimensions of about 2.3 mm, corner pores, rare mid-wall pores, and short septal spines; Stearn's illustrations show coralla that seem to have much more densely spaced tabulae and more abundant mid-wall pores than does *P. subelongus*. Stearn (1956, p. 61, pl. 10, fig. 12) also described *P. capax* from the upper members of the Stony Mountain Formation and from the Stonewall Formation. This has much larger corallites with adult dimensions of about 3.8 mm, very thin walls, and rare or absent septa.

Nelson (1963) described *Palaeofavosites* [*sic*] *prolificus* from members 1 and 2 of the Chasm Creek Formation, Hudson Bay Lowland, northern Manitoba (Richmondian; see Elias, 1991, fig. 3). We examined Nelson's illustrated specimen, which he collected in 1950 (GSC 10329); it is very similar to *P. subelongus*, having moderately thin-walled, regular-sized corallites that appear to lack septa and have corner pores only (biometric data: ACD (all) = 1.74 mm, ACD (6+) = 1.79 mm, CoA = 2.74 mm^2; see Text-fig. 27). It is listed with a *confer* in our synonymy. Nelson (1963, pp. 52–53, pl. 7, fig. 4) also documented *Palaeofavosites* [*sic*] *capax* from member 1 and the upper member of the Caution Creek Formation and from the Chasm Creek Formation, Hudson Bay Lowland, northern Manitoba (all Richmondian; see Elias, 1991, fig. 3). This species is very different, having very large mature corallites with dimensions of about 4–5 mm.

Paleofavosites sp. cf. *P. capax* was described but not illustrated by Pandolfi (1985, pp. 28, 29) from the Upper Ordovician Lost Canyon and Floride members of the Ely Springs Dolomite of Nevada and Utah. This material is distinguished from *P. subelongus* by its larger corallites with dimensions of 1.5–4.2 mm.

Laub (1979, pp. 263–271, pl. 9, figs. 1–5, pl. 29, figs. 3, 4, pl. 39, figs. 1, 3) described a *P. prolificus* from the mid-Llandovery Brassfield Formation of Ohio and possibly of Indiana and Kentucky. This species is not very similar to *P. subelongus*. It has corallites of regular size with dimensions of about 1.0–1.5 mm and, according to the description, possesses corner pores only.

One illustration (Laub, 1979, pl. 29, fig. 4), however, shows common mid-wall pores in some parts of a corallum.

Another species similar to *P. subelongus* is *Paleofavosites nodosus* Poulsen (1941, p. 22, pl. 4, figs. 4–6), from the Offley Island Formation of north Greenland (Upper Llandovery). The latter species has corallites of variable size, the larger ones with dimensions of about 2.0–2.5 mm, and has corner pores only. The illustrations are not sufficiently clear for more detailed comparisons.

Among the other species occurring in the uppermost Ordovician and lowermost Silurian of the east-central United States, *P. subelongus* shares some characters with *Paleofavosites* sp. cf. *P. subelongus, Paleofavosites* sp. cf. *P. ivanovi,* and *Paleofavosites* sp. A. Comparisons are included in the *Discussion* under each of those species.

Occurrences.—Uppermost Ordovician (Gamachian): lower Keel Formation, south-central Oklahoma; Leemon Formation, southern Illinois. Uppermost Ordovician (Gamachian) to lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): Cyrene Formation, northeastern Missouri. Uppermost Ordovician (?; Gamachian?) to lowermost Silurian (Lower Llandovery, lower Rhuddanian): Wilhelmi Formation, northeastern Illinois; lower Mosalem Formation, northwestern Illinois. Lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): unnamed member and Kissenger Limestone Member, Bryant Knob Formation, northeastern Missouri.

Possibly in lowermost Silurian (Lower Llandovery, lowermost Rhuddanian): lower part of member 1, Becscie Formation, Anticosti Island, Québec.

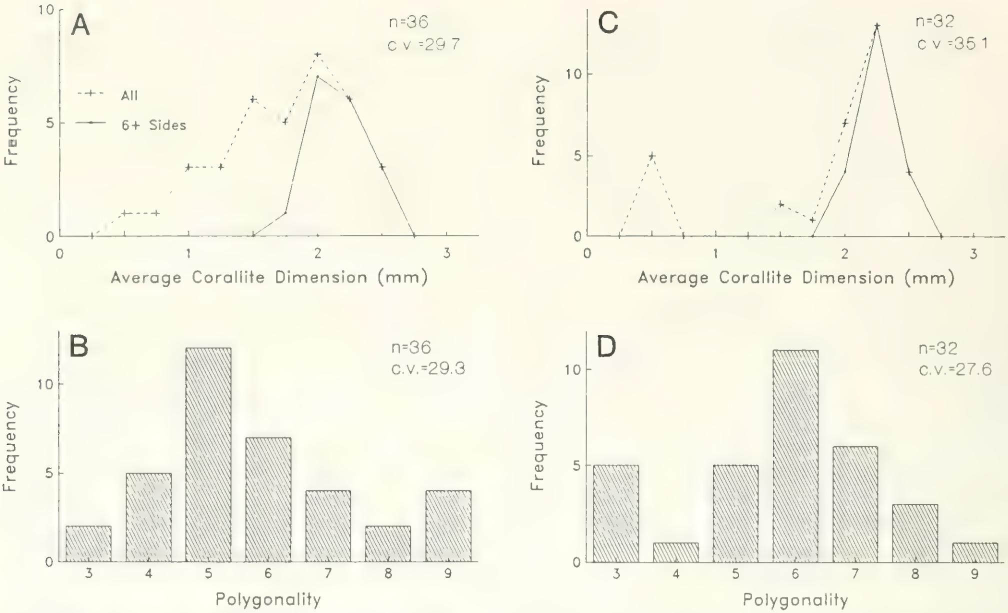
Holotype.—UI X-878a (Savage, 1913, pl. 3, fig. 10; Savage, 1917, pl. 5, fig. 10; Pl. 13, figs. 8, 9), collected by T. E. Savage (labelled "*Favosites subelongus,* Silurian, Edgewood [Formation], 3 mi. S. of Clarksville, Mo."), Bryant Knob Formation, 5 km south of Clarksville, Pike County, Missouri.

Other material described above.—144 specimens: USNM 485785a, site 23iv, interval 23-2 (*Brevilamnulella* beds), USNM 458776, 485816, site 23i, interval 23-3, Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; USNM 485817, interval 21-1b, Ideal Quarry Member, Keel Formation, Section 21 (Rock Crossing), Carter County, Oklahoma; USNM 485818–485823, interval 31-1, Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois; USNM 485824–485826, interval 18-1, unnamed member, USNM 485827, interval 18-2, Kissenger Limestone Member, Bryant Knob Formation, Section 18 (Kissenger), Pike County, Missouri; UI X-878b, C-1466a, collected by T. E. Savage (labelled "*Favosites subelongus,* Edgewood [Formation], 3 mi. S. of Clarksville, Mo."), UI C-1462b, collected by T. E. Savage (labelled "*Lyellia thebesensis,* Edgewood [Formation], 3 mi. S. Clarksville, Mo."), UI C-1465a, C-1465b, collected by T. E. Savage (labelled "*Calapoecia favositoidea,* Edgewood [Formation], 3 mi. S. Clarksville, Mo."), Bryant Knob Formation, 5 km south of Clarksville, Pike County, Missouri; USNM 459086, 485828, interval 16-1, Kissenger Limestone Member, Bryant Knob Formation, Section 16 (Clinton Spring), Pike County, Missouri; UI X-771, collected by T. E. Savage (labelled "*Calopoecia* [*sic*] *favositoidea,* Edgewood [Formation], Louisiana"), Bryant Knob Formation, Louisiana, Pike County, Missouri; USNM 459074, 485829–485835, 485836a–c, interval 15-1, Kissenger Limestone Member, Bryant Knob Formation, Section 15 (Calumet), Pike County, Missouri; USNM 459078, 459079–459081, 459082, 485812a, 485837–485856, 485857a, 485857b, 485858a–d, 485859–485873, interval 14-1, Kissenger Limestone Member, Bryant Knob Formation, Section 14 (Higginbotham Farm), Pike County, Missouri; USNM 485874, 485875, interval 13-0, Cyrene Formation, Section 13 (Bowling Green), Pike County, Missouri; UI C-1457, collected by T. E. Savage (labelled "*Calapoecia favositoidea,* Edgewood [Formation], near Edgewood, Mo."), UI C-1458b–g, collected by T. E. Savage (labelled "*Calapoecia favositoidea,* Edgewood Ls., near Edgewood, Mo."), Cyrene Formation, near Edgewood, Pike County, Missouri; USNM 485876, 485877, interval 37-1, Wilhelmi Formation, Section 37 (Essex), Kankakee County, Illinois; UI C-162a, C-162b, collected by T. E. Savage (labelled "*Favosites subelongus,* Edgewood ls., [locality] A-1C"), UI C-1592, collected by T. E. Savage (labelled "*Favosites subelongus,* 1 mi. below Channahon ls. otc."), Wilhelmi Formation, 3.2 km south of Channahon, Will County, Illinois; USNM 485878, 485879, 485880a, 485880b, 485881–485926, interval 32-1z, Mosalem Formation, Section 32 (Thomson East), Carroll County, Illinois.

Paleofavosites species cf. **P. subelongus**
(Savage, 1913)
Plate 17, figures 8–12

Description.—Coralla have low domical and low and high bulbous growth forms (Table 14). Size range is 31–43 mm wide and 20 to more than 30 mm high.

In transverse section, corallites appear as polygons of regular or slightly irregular shape (Pl. 17, figs. 9, 11). Average corallite dimensions are variable, 0.4–3.0 mm; average dimensions of adult corallites are commonly 1.5—2.6 mm (Table 19). Mean corallite areas on transverse sections are about 2–4 mm^2 (Table 19). New corallites have three or four sides; sides were added



Text-figure 28.—Frequency distributions of average corallite dimension (all corallites and those with six and more sides) and polygonality for two coralla of *Paleofavosites* sp. cf. *P. subelongus*. **A**, **B**, USNM 485930, **C**, **D**, USNM 485932, both from Section-interval 32-1c (Thomson East). Each pair of graphs represents the same single transverse section; n = number of corallites (all), c.v. = coefficient of variation for all corallites.

with growth, and mature individuals commonly have up to eight or nine sides, rarely up to 12 sides (Table 19). On most transverse sections, a considerable degree of variability of corallite shapes and sizes occurs (Pl. 17, figs. 9, 11; see *Intraspecific variation,* below). In longitudinal section, corallites are straight, or may be gently curved away from the colony axis.

Corallite walls are straight or broadly curved (Pl. 17, fig. 9). Walls appear to be thin to moderately thick, but thickness and structure could not be accurately determined due to poor preservation. Corner pores and mid-wall pores are both rare to common (Pl. 17, figs. 8, 11). Corner pores are simple, with diameters of 0.1–0.2 mm (Table 19). The end of a wall adjacent to a corner pore is often square and bulges slightly. Mid-wall pores have diameters of about 0.1–0.2 mm.

In transverse section, septa are short (Pl. 17, fig. 9) to moderately long and thorn-like, or absent (Pl. 17, fig. 11). They are slightly upturned adaxially, and often have thickened bases. Tabulae are thin; flat, wavy, or slightly convex or concave (Pl. 17, figs. 10, 12). They are usually complete, rarely incomplete. Tabulae are often quite broadly spaced, averaging about five in 5 mm (Table 19); in some coralla, tabular spacing shows marked periodicity, with distinct horizontal bands having much denser spacing of tabulae.

Intraspecific variation.—This collection shows quite a high degree of variability in corallite size and polygonality. Corallite size-frequency distributions on transverse sections show one or more modes (Text-fig. 28A, C). For coralla having bimodal or polymodal distributions, adult corallites with six and more sides show a virtually normal distribution under the largest mode. In one corallum, the frequency distribution for polygonality roughly parallels that for corallite dimensions (Text-fig. 28C, D). Such a relationship is not apparent in another specimen because the size mode representing adult individuals is spread more evenly among corallites having six to nine sides (Text-fig. 28A, B).

Average corallite dimensions for all corallites and for those corallites with six and more sides on transverse sections show a positive correlation (Text-fig. 27, *Paleofavosites* sp. cf. *P. subelongus*). There is a considerable degree of variation in these characters among the seven measured coralla; the most disparate transverse section is from a corallum for which a second section plots close to those for the other coralla.

Discussion.—The coralla described above are similar to the older *Paleofavosites subelongus* (latest Ordovician–earliest Silurian) in all characters except mid-wall pores, which are rare in *P. subelongus* but are common in this collection. For that reason, and because of poor preservation, these specimens are identified as *Paleofavosites* sp. cf. *P. subelongus.* They are especially similar to the coralla of *P. subelongus* occurring lower in the Mosalem Formation at the same locality, Section 32 (Thomson East) (Pl. 17, figs. 4–7; see Text-figs. 25A, 27). As described elsewhere (see *P. subelongus,* p. 40), mid-wall pores have not been seen in definitely Ordovician members of *P. subelongus,* but appear in the earliest Silurian. The increased abundance of this character through time seems to represent a phyletic trend, and *Paleofavosites* sp. cf. *P. subelongus* probably evolved from *P. subelongus.*

See the *Discussion* under *P. subelongus* (pp. 87–89) for comparisons with other species.

Occurrence.—Lower Lower Silurian (Lower Llandovery, upper Rhuddanian): upper Mosalem Formation, northwestern Illinois.

Material described above.—Nine specimens: USNM 485927–485935, interval 32-1c, Mosalem Formation, Section 32 (Thomson East), Carroll County, Illinois.

Paleofavosites adaensis, new species
Plate 18, figures 1–11

Derivation of name.—This species is named for the town of Ada, Oklahoma, which is 12 km north-northeast of the type locality.

Diagnosis.—*Paleofavosites* with large corallites, adult average corallite dimensions commonly 3.2–5.5 mm; corallite sizes and shapes often regular. Walls thin. Corner pores and mid-wall pores both rare to common. Septa absent or consisting of rare, short spines. Tabulae often crenulate, of variable form, complete or incomplete. Coralla commonly have basal holothecae.

Description of coralla.—Two measured coralla are tabular (Table 14), 45–125 mm wide and 7–20 mm high. Other coralla are broken, but appear to have had low domical and bulbous growth forms.

In transverse section, corallites are polygonal, often of regular size (Pl. 18, fig. 5). Average corallite dimensions are 0.6–5.8 mm; average dimensions of adult corallites are commonly 3.2–5.5 mm (Table 19). Mean corallite areas on transverse sections are about 8–17 mm^2 (Table 19). Corallites have three to 10 sides (Table 19). Distribution of corallite shapes depends on variability of average corallite dimensions; in most transverse sections, the majority of corallites have regular sizes and have five to seven sides (Pl. 18, fig. 5); in other sections, large corallites with eight or nine sides are interspersed in places with small individuals having three or four sides (Pl. 18, fig. 9; see *Intraspecific variation,* below). In longitudinal section, corallites are straight or gently curved, occasionally geniculate.

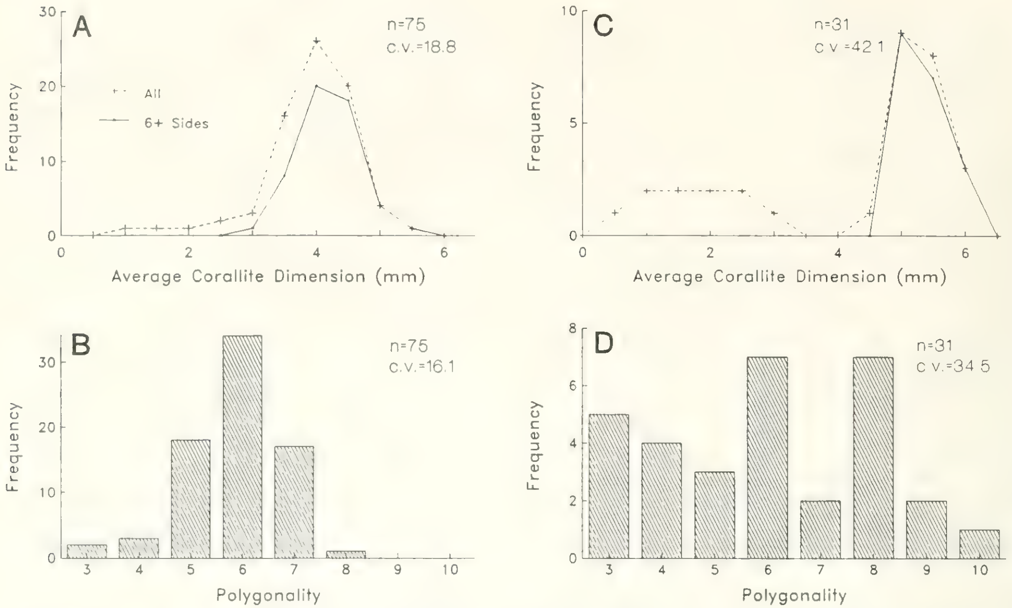
Corallite walls are straight, slightly curved, or wavy in transverse section (Pl. 18, fig. 5). Walls are usually thin, but thickness is variable, commonly 0.025–0.075 mm (Table 19). In longitudinal section, walls are wavy (Pl. 18, figs. 4, 10). Corner pores and mid-wall pores are both rare to common. Corner pores are simple, commonly with diameters of 0.1–0.3 mm (Table 19). In some cases the free end of the wall adjacent to a corner pore is rounded (Pl. 18, fig. 8). Mid-wall pores are arranged in one or two vertical rows per wall; diameters are about 0.15–0.30 mm. The end of a wall adjacent to a mid-wall pore may be slightly rounded (Pl. 18, fig. 7) or square. Septa are generally absent; short spinose septa occur rarely in some coralla (Pl. 18, fig. 3).

Tabulae are thin, crenulate, slightly convex, concave, or irregular, and complete or incomplete (Pl. 18, figs. 3, 4, 10). Tabulae often have abaxial upward deflections near the wall. Tabular spacing varies among localities; spacing may be very close or quite broad, averaging about five tabulae in 5 mm (Table 19). Tabulae may appear as partial or complete rings in transverse section, or their crenulate margins may appear as a series of arcuate lines.

Astogeny and corallite increase.—Descriptions are based largely on a single serial-sectioned corallum (USNM 485937). Other specimens are used for comparison.

The absolute base of the serial-sectioned corallum is unknown. In other specimens, corallites may extend upward from broad basal holothecae, or there may be a small group of corallites that apparently grew from a single point prior to the expansion of a basal holotheca (Pl. 18, figs. 2, 3). In some cases the basal holotheca has short spines on its upper surface (Pl. 18, fig. 2). Corallites are large and regular in the lowest known parts of the serial-sectioned corallum (see *Intraspecific variation,* below). During subsequent growth, cyclomorphic variation is represented mostly by changes in spacing of tabulae (Pl. 18, figs. 4, 10); there is little variation in thickening of skeletal elements with height in a corallum. In most specimens, some corallites extend through most or all of the height of a corallum. Dense tabular spacing occurs at the uppermost surfaces of some coralla.

Corallite increase is intracalicular and peripheral. Offsets are generally rare in mature parts of each cor-



Text-figure 29.—Frequency distributions of average corallite dimension (all corallites and those with six and more sides) and polygonality for two coralla of *Paleofavosites adaensis*. **A**, **B**, USNM 485937 (paratype), Section-interval 35-1 (Henry House Falls). **C**, **D**, UI C-1351, Alexander County, Illinois. Each pair of graphs represents the same single transverse section; n = number of corallites (all), c.v. = coefficient of variation for all corallites.

allum, but may be locally common. Most new offsets have four sides, and each was initiated along one wall of the parent corallite. Three-sided offsets are rarer; each was initiated in a corner of the parent corallite. Groups of offsets occur where a colony regenerated following partial mortality. Such offsets can have four or five sides; walls that are not in contact with other corallites are curved (Pl. 18, fig. 6). All offsets added sides as they grew.

Coralla show some lateral spreading, but much growth was regular and vertical. Offsetting is concentrated at the absolute corallum margins, and in zones of regeneration following partial colony mortality (Pl. 18, fig. 6); in both locations, considerable areas tend to be covered by offsets only. Zones of partial mortality are often represented by sediment inclusions within the corallum (Pl. 18, fig. 4); regeneration was accomplished through the expansion of a holotheca across a sediment inclusion, with new corallites being initiated across the upper surface of the holotheca. Bands of very dense tabular spacing often occur immediately below and adjacent to sediment inclusions (Pl. 18, fig. 4). Since much corallum growth was vertical, there is little character variation between the axis and margins.

Microstructure.—The wall between each pair of corallites is composed of three layers: a dark median line bounded on either side by a paler radially fibrous layer (Pl. 18, figs. 5, 7, 8). The median line appears to have a lamellar microstructure and has definite lateral boundaries. It is usually slender, but may thicken slightly at wall junctions. The fibrous wall layers consist of fibers that are perpendicular to the wall in transverse section, and are perpendicular or directed upward laterally from the median line at angles of up to 30° in longitudinal section.

The holotheca consists of an inner fibrous layer and a darker, apparently lamellar outer (basal) layer (Pl. 18, fig. 2). Fibers in the fibrous layer are oriented approximately perpendicular to the holotheca. In one corallum, short fibrous spines project upward from the fibrous layer (Pl. 18, fig. 2). The darker outer layer is about the same thickness as the dark median line in a corallite wall, and has a similar texture and appearance to that of the dark line.

Microstructure of tabulae is indistinct. Lateral margins of tabulae are embedded in the outer fibrous wall.

Intraspecific variation.—Analysis of variation was limited by the small number of specimens available.

There is little variation between coralla or between localities in several characters, including septal development, wall thickness, and form of pores. Other characters, such as corallite size and spacing of tabulae, are obviously different between localities (see below).

In general, frequency distributions for transverse sections above the basal part of each corallum show a predominance of adult corallites (Text-fig. 29A, C). This reflects the concentration of most offsetting at or near the base of each corallum. The slight differences in distribution of average corallite dimensions between the two coralla in Text-figure 29 reflect variations in growth pattern. Virtually all offsetting in a tabular corallum (Text-fig. 29A) was basal, but in a corallum that apparently had a bulbous form later offsetting also occurred (Text-fig. 29C). Distributions of corallite polygonality (Text-fig. 29B, D) parallel those for average corallite dimension, reflecting the addition of sides to corallites as they expanded. There is also a positive correlation between the average dimension of all corallites and the corallite dimension of those having six or more sides on the same transverse section (Text-fig. 27).

Variation in these and some other characters is distinctly related to locality. Specimens from Section-interval 23-5 (Lawrence Quarry) are similar to those from the Sexton Creek Limestone in southern Illinois (UI C-1347, C-1351). Coralla from both collections show somewhat variable corallite size distributions in conjunction with widely spaced tabulae (see Pl. 18, figs. 1, 3, 9, 10); growth forms are bulbous or domical. Coralla from Section-interval 35-1 (Henry House Falls) are different, having regular corallite size distributions and densely spaced tabulae (Pl. 18, figs. 4, 5); their growth forms are tabular (see *Paleofavosites adaensis,* p. 40).

Discussion.—These coralla are assigned to a new species, *Paleofavosites adaensis.* This species is an early member of a group of large-corallite favositids similar to *Favosites gothlandicus* Lamarck. Members of this group occur from the earliest Silurian (earliest Llandovery) until the early Late Silurian (Ludlow), and possible members occur both earlier and later. Position of pores varies within this group, but other characters are quite consistent. These include thin walls, short septa, and corallites of large size and regular size distribution.

Some of the Ordovician corals described as *Paleofavosites capax* are similar to members of this group. The most similar is Bolton's (1980, pp. 22, 25, pl. 2.7, figs. 1, 5, 6) material from the Burmingham Member of the White Head Formation near Percé, Québec (Upper Ordovician, Ashgill, pre-Hirnantian; see Skidmore and Lespérance, 1981, p. 38; Lespérance *et al.,* 1987, fig. 4). It has adult corallites with dimensions of 3.3–4.0 mm, thin walls, and some mid-wall pores, and lacks septal spines, but differs from *P. adaensis* by having much more abundant small corallites on transverse sections. Other corals referred to *P. capax* are listed in the *Discussion* under *P. subelongus* (pp. 87, 88).

Among other Early Llandovery species, *P. adaensis* is most similar to *Paleofavosites* sp. of Bolton (1981b, pl. 1, fig. 3), from the Clemville Formation of the southern Gaspé Peninsula, Québec (Lower–Middle Llandovery, Rhuddanian–lower Aeronian; Nowlan, 1983, fig. 2, termed Rhuddanian–Idwian therein). Bolton's species has similar thin-walled corallites of regular size, but these are slightly smaller with dimensions of about 2.5–3.3 mm, and appear to have corner pores only.

Another similar species is *Palaeofavosites* [*sic*] *oelaensis* Klaamann (1959, p. 259, pl. 2, figs. 3, 4), from the Juuru Stage of Estonia (Rhuddanian), also described and illustrated by Stasinska (1967, p. 71, pl. 14, figs. 1a, 1b, table 4) from Spirodden, Asker district of Norway (Llandovery 6cα: lower Aeronian; upper Solvik Formation?; Worsley *et al.,* 1983, fig. 5). Klaamann's and Stasinska's coralla have corallites with dimensions of 2.6–4.2 mm and 1.5–4.2 mm, respectively, and possess both mid-wall and corner pores. They differ from *P. adaensis* by apparently having common, short septal spines, and corallites that may have variable sizes and shapes in transverse section. *Favosites ingens* Klaamann (1962, pp. 162, 163, pl. 5, figs. 1, 2) from the Adavere Stage of Estonia (Upper Llandovery, Telychian), also described and illustrated by Stasinska (1967, pp. 80, 81, pl. 20, figs. 1–4) from the Upper Llandovery of Ringerike and Malmøy, Norway (Series 7), has mid-wall pores only, and large corallites with dimensions of about 4.0–8.0 mm.

Copper (1978, pl. 10, figs. 4, 5) illustrated a coral identified as *Favosites* sp. from the Fossil Hill Formation of Manitoulin Island, Ontario (Telychian; Brett *et al.,* 1991, fig. 5). This species has large, thin-walled corallites with regular dimensions of about 5–6 mm. Pores could not be recognized in the photographs, but the assignment to *Favosites* suggests that it lacks the corner pores characteristic of *P. adaensis.*

Palaeofavosites [*sic*] *asper* var. *maxima* Chernyshev (1937, p. 84, pl. 6, fig. 5) from the Upper Silurian of Novaya Zemlaya has also been described and illustrated as *Palaeofavosites* [*sic*] *maximus* by Kokscharskaya (in Volkova *et al.,* 1978, pp. 41, 42, pl. 9, figs. 1a, 1b) from the Kuranakhinskiy Horizon of Verkhoyan, Siberia (Lower–Middle Llandovery). Chernyshev's material has corallites of regular size with diameters of about 4–5 mm, and weak septa, but other features are difficult to determine. Kokscharskaya's specimens have corallites with dimensions of 3.5–4.2 mm, and some mid-wall pores, but they are distinguished from *P. adaensis* by having non-crenulate tabulae, thicker walls, and small corallites that are more abundant.

The neotype of *Favosites gothlandicus,* from the Mulde Marl of Gotland, Sweden (upper Lower Silurian, Upper Wenlock), was described and illustrated by Jones (1936, pp. 8, 9, pl. 1, figs. 1, 2) and by Lafuste and Tourneur (1988, pp. 189–198, figs. 1–4, pl. 1, figs. 1–4, pl. 2, figs. 1–3). This corallum is somewhat similar to *P. adaensis,* having corallites of regular size with thin walls and lacking septa, but has smaller corallites with dimensions commonly 2.0–2.7 mm and sometimes up to 3.2 mm, and mid-wall pores only. Many of the other Late Llandovery, Wenlock, and Ludlow corals that have been assigned to *F. gothlandicus* by various authors bear some similarity to *P. adaensis,* but all are distinguished from it by their lack of corner pores. The true nature of all material previously described as *F. gothlandicus* presents a substantial taxonomic problem that is outside the scope of the present study.

Within the group of large-corallite favositids similar to *F. gothlandicus,* a transition in position of pores occurred through time. The earliest species, including *P. adaensis,* are members of *Paleofavosites* possessing only corner pores or a combination of corner and mid-wall pores. Later species have exclusively mid-wall pores and belong to *Favosites.* It is quite possible that the change in pore position in this lineage occurred independently from parallel changes taking place in other favositids.

Among the other species occurring in the east-central United States, *P. adaensis* is most similar to *Paleofavosites* sp. cf. *P. ivanovi.* The latter species occurs in the Bowling Green Dolomite of west-central Illinois and northeastern Missouri, and is of approximately equivalent age to *P. adaensis* (*i.e.,* late Rhuddanian). It is distinguished from *P. adaensis* by its smaller corallites (see Text-fig. 27; Table 19), less regular corallite size distributions on transverse sections, and much rarer mid-wall pores.

Paleofavosites adaensis was listed by Elias and Young (1992, fig. 2) as *Paleofavosites* n. sp. A, and by Young and Elias (1993) as *Paleofavosites* n. sp.

Occurrences.—Lower Lower Silurian (Lower Llandovery, upper Rhuddanian): upper Mosalem Formation, northwestern Illinois. Lower Lower Silurian (Lower? Llandovery, upper Rhuddanian?): Cochrane Formation, south-central Oklahoma; Sexton Creek Limestone, southern Illinois.

Holotype.—USNM 485936 (Pl. 18, figs. 1–3), site 23i, interval 23-5, Cochrane Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma.

Paratype.—USNM 485937 (Pl. 18, figs. 4–8), interval 35-1, Cochrane Formation, Section 35 (Henry House Falls), Carter County, Oklahoma.

Other material described above.—Six specimens: USNM 485938, site 23i, interval 23-5, Cochrane Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; USNM 485939, 485940, interval 35-1, Cochrane Formation, Section 35 (Henry House Falls), Carter County, Oklahoma; UI C-1347, C-1351, collected by T. E. Savage (labelled "*Favosites favosus* Goldfuss, Sexton Creek [Formation], Alexander Co., Ill."), Sexton Creek Formation, Alexander County, Illinois; USNM 485941, interval 10-3, Mosalem Formation, Section 10 (Lost Mound), Jo Daviess County, Illinois.

Paleofavosites species
cf. **P. ivanovi** Sokolov, 1951a
Plate 19, figures 1–7

[*cf.*] *Palaeofavosites ivanovi* Sokolov, 1951a, pp. 37, 38, pl. 3, figs. 2, 3; Sokolov and Tesakov, 1963, p. 43, pl. 2, figs. 1, 2.

[?] *Paleofavosites capax* (Billings, 1866). Bolton, 1981a, pl. 9, fig. 10.

Description.—Growth form can be examined in one corallum (USNM 485942). It has a low domical form, and is more than 27 mm wide and 19 mm high.

In transverse section, corallites are usually regular polygons (Pl. 19, fig. 1). Average corallite dimensions are variable on each transverse section (Text-fig. 30A): overall range is 0.50–4.25 mm; average dimensions of adult corallites are commonly 2.7–4.0 mm (Table 19). Mean corallite areas on transverse sections are about 5–6 mm^2 (Table 19). Corallites may have three to ten sides (Table 19); shapes are variable on each transverse section, reflecting the variability of average dimensions (Pl. 19, figs. 1, 7; see Text-fig. 30A, B). Corallites at the colony margin have flat outlines where they are in contact with other individuals, but are curved on their free sides (Pl. 19, fig. 2). In longitudinal section, corallites curve gently away from the colony axis (Pl. 19, fig. 6).

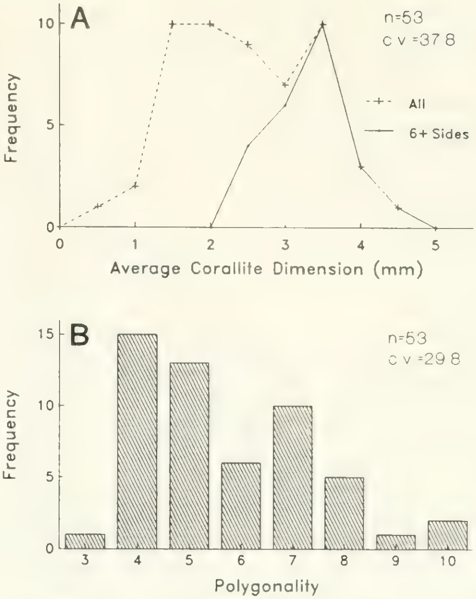
Corallite walls are straight or curved in transverse section, rarely wavy (Pl. 19, fig. 4). Walls are thin, 0.05–0.10 mm thick (Table 19); thickness is regular. In longitudinal section, walls are straight or wavy (Pl. 19, figs. 3, 6). Corner pores are moderately common; they are simple, with diameters of 0.075–0.175 mm (Table 19). The end of a wall adjacent to a pore may be square. Corner pores usually have thin pore plates that are straight or are broadly curved into corallite lumina. Mid-wall pores located a short distance in from the wall corner occur in a few corallites.

Septa are generally absent, but short, slender septal spines are developed locally in zones that show slight cyclomorphic thickening. In longitudinal section, spines are straight, and are directed slightly upward adaxially (Pl. 19, fig. 6). Average length of septa is 4% of corallite radius (Table 19). Tabulae are moderately thin, flat or wavy, and may have lobe-like axial depressions (Pl. 19, figs. 3, 6). They are usually complete. Some tabulae are crenulate, appearing as curved plates along the corallite wall in transverse section (Pl. 19, fig. 4). Tabulae are very widely spaced, about two in 5 mm (Table 19).

Discussion.—These coralla are comparable to *Palaeofavosites* [*sic*] *ivanovi* from the Upper Ordovician of the west slopes of the Urals (Sokolov, 1951a), and from the Upper Ordovician (mid–upper Ashgill) Burskiy Horizon (Bur Formation; Kanygin *et al.*, 1988, p. 11) of the Siberian Platform (Sokolov and Tesakov, 1963). As described and illustrated, *P. ivanovi* has corallites of variable size, the larger ones with dimensions of about 2.5–3.5 mm, and appears to have only rare, short septa. It differs from our coralla by having thicker walls, tabulae that are generally more densely spaced, and larger corner pores. Specimens from the east-central United States are therefore identified as *Paleofavosites* sp. cf. *P. ivanovi.*

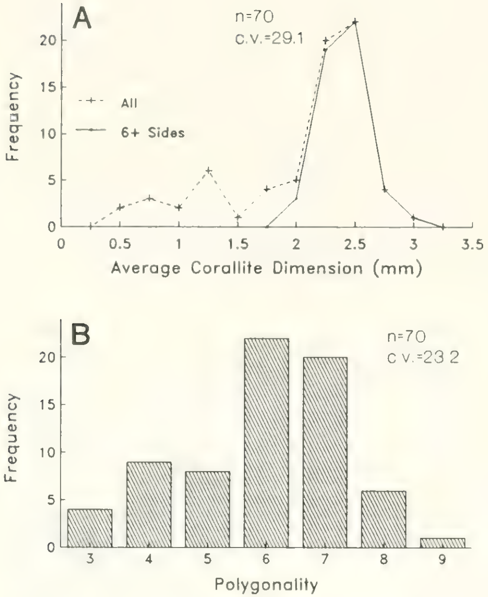
Our material is very similar to, and is questionably synonymized with a corallum from the Gun River Formation of Anticosti Island, Québec (lower Lower Silurian, Middle Llandovery, lower Aeronian; Barnes, 1988, fig. 2), illustrated as *Paleofavosites capax* by Bolton (1981a). We examined that specimen, collected by Bolton in 1975 (GSC 66875); like *Paleofavosites* sp. cf. *P. ivanovi,* it also has corallites of variable size, short and rare septa, thin walls, and broadly spaced crenulate tabulae, but differs by having more abundant mid-wall pores and smaller corallites (biometric data: ACD (all) = 1.92 mm, ACD (6+) = 2.63 mm, CoA = 3.85 mm^2, Pol = 6.1, WT = 0.106 mm, LS = 0%, Ta5 = 1.4; compare with Table 19; see Text-fig. 27).

Other similar species include *Palaeofavosites* [*sic*] *alveolaris* (Goldfuss) and *Palaeofavosites* [*sic*] *spiroddensis* Stasinska, as documented by Stasinska (1967, pp. 67, 72, table 4, pl. 15, figs. 2, 3a, 3b, 4a–c) from the Llandovery Series 6 of Norway (Lower–Middle Llandovery, Rhuddanian–lower Aeronian; Worsley *et al.*, 1983, fig. 5, termed Rhuddanian–Idwian therein). These species have corallites of variable size, crenulate tabulae, and short, thin septa; they may be conspecific with one another. They differ from *Paleofavosites* sp. cf. *P. ivanovi* by having smaller corallites with dimensions of about 2.5–3.0 mm, and more densely spaced tabulae. *Palaeofavosites* [*sic*] *alveolaris* (Lonsdale), as described and illustrated by Nelson (1963, pp. 51, 52, pl. 7, fig. 9) from member 3 and the upper member of the Caution Creek Formation and from members 1 and 2 of the Chasm Creek Formation of northern Manitoba (Upper Ordovician, Richmondian; see Elias, 1991, fig. 3), is quite different, having corallites of regular size and shape (see *Discussion* under *Paleofavosites* sp. A, p. 96).



Text-figure 30.—Frequency distributions of average corallite dimension (all corallites and those with six and more sides) and polygonality for one corallum of *Paleofavosites* sp. cf. *P. ivanovi.* **A, B,** USNM 485943, Section-interval 17-1a (Clarksville). Both graphs represent the same transverse section; n = number of corallites (all), c.v. = coefficient of variation for all corallites.

Among the other species occurring in the uppermost Ordovician and lowermost Silurian of the east-central United States, *Paleofavosites* sp. cf. *P. ivanovi* has some similarities to both the older *Paleofavosites subelongus* and to *Paleofavosites adaensis,* which is of approximately equivalent age. *Paleofavosites subelongus* also tends to have corallites of variable size, but these are somewhat smaller than those of *Paleofavosites* sp. cf. *P. ivanovi* (Text-fig. 27) and have thicker walls and longer, more abundant septa. *Paleofavosites adaensis* is similar to *Paleofavosites* sp. cf. *P. ivanovi* in having thin walls and septa that are weak or absent, but has larger corallites (Text-fig. 27) that are usually of regular size, and more abundant mid-wall pores.



Text-figure 31.—Frequency distributions of average corallite dimension (all corallites and those with six and more sides) and polygonality for one corallum of *Paleofavosites* sp. A. **A, B**, USNM 485947, Section-interval 6-1 (Plaines West). Both graphs represent the same transverse section; n = number of corallites (all), c.v. = coefficient of variation for all corallites.

Occurrences.—Lower Lower Silurian (Lower Llandovery, upper Rhuddanian): Bowling Green Dolomite, northeastern Missouri and west-central Illinois.

Possibly in lower Lower Silurian (Middle Llandovery, lower Aeronian): Gun River Formation, Anticosti Island, Québec.

Material described above.—Two specimens: USNM 485942, interval 36-1, Bowling Green Dolomite, Section 36 (Indian Creek), Calhoun County, Illinois; USNM 485943, interval 17-1a, limestone facies at base of Bowling Green Dolomite, Section 17 (Clarksville), Pike County, Missouri.

Paleofavosites species A

Plate 19, figures 8–12

Description.—Coralla have tabular and low domical growth forms (Table 14). Size range is 47–115 mm wide and 14–40 mm high.

In transverse sections, corallites appear as polygons of regular or slightly irregular shape (Pl. 19, figs. 9, 11). The overall range of average corallite dimensions is 0.55–2.82 mm; adult corallites commonly have average corallite dimensions of 2.0–2.7 mm (Table 19). Mean corallite areas on transverse sections are about 3–4 mm^2 (Table 19). On transverse sections, most corallites have regular sizes and have five to seven sides; corallites may rarely have up to nine sides (Pl. 19, figs. 9, 11; Text-fig. 31A, B; Table 19). Offsets are relatively rare, and commonly have three or four sides; sides were added during growth. There is little variation among the studied coralla in average corallite dimensions (Text-fig. 27). In longitudinal section, corallites are straight or slightly curved.

Corallite walls are straight or gently curved in transverse section (Pl. 19, fig. 9). Walls are thin; 0.050–0.125 mm thick (Table 19). Walls are straight or wavy in longitudinal section (Pl. 19, figs. 10, 12). Corner pores are simple, and mid-wall pores may occur, but poor preservation prevents detailed observation. Septa are generally absent (Table 19); short, thick septal spines occur rarely. Tabulae are strongly crenulate; concave in corallite corners, and at midpoint of wall in large corallites (Pl. 19, fig. 8). Spacing of tabulae is variable, averaging about four in 5 mm (Table 19). In some coralla, spacing of tabulae shows well-developed cyclomorphic variation; in one corallum, pairs of closely spaced and widely spaced bands average 18.5 mm in thickness (Table 19; Pl. 19, fig. 12).

Discussion.—These coralla are identified as *Paleofavosites* sp. A; their poor preservation prevents a definite specific assignment and makes comparisons with other species difficult. They are probably most similar to *Palaeofavosites* [*sic*] *argutus* Ivanov (1950, p. 14, pl. 3, figs. 1, 2) from the Upper Ordovician of the Urals, also described and illustrated by Sokolov and Tesakov (1963, pp. 40, 41, pl. 1, figs. 1, 2) from the Upper Ordovician of the Siberian Platform. Both of those studies described corals with corallite dimensions of about 2.0–2.5 mm. It is difficult to determine details from Ivanov's illustrations; Sokolov and Tesakov's material has corallites of regular size with a very similar appearance to those of *Paleofavosites* sp. A, but may have thicker walls.

Paleofavosites sp. A is also similar to *Palaeofavosites* [*sic*] *alveolaris* as described and illustrated by Nelson (1963, pp. 51, 52, pl. 7, fig. 9) from member 3 and the upper member of the Caution Creek Formation and from members 1 and 2 of the Chasm Creek Formation of northern Manitoba (Upper Ordovician, Richmondian; see Elias, 1991, fig. 3). Nelson's material has corallites of regular size and apparently lacks septa, but the corallites are slightly larger (dimensions of about 2.5–3.0 mm) than those in our specimens, and the tabulae are described as flat, not crenulate. *Paleofavosites* sp. A is not similar to the *Palaeofavosites* [*sic*] *alveolaris* described and illustrated by Stasinska (1967,

p. 67, pl. 15, figs. 2, 3a, 3b, table 4) from the Llandovery Series 6 of Norway (lower Lower Silurian, Lower–Middle Llandovery, Rhuddanian–lower Aeronian; Worsley *et al.*, 1983, fig. 5, termed Rhuddanian–Idwian therein) (see *Discussion* under *Paleofavosites* sp. cf. *P. ivanovi*, p. 95).

Paleofavosites sp. A is somewhat similar to, and may have been descended from, the older *Paleofavosites subelongus*, which occurs in the uppermost Ordovician and lowermost Silurian of the east-central United States. It is distinguished from *P. subelongus* by its regular-sized, large corallites, generally thinner walls and rare or absent septa, and typically lower growth forms.

Occurrence.—Lower Lower Silurian (Lower–Middle Llandovery, upper Rhuddanian–lowermost Aeronian): Elwood Formation, northeastern Illinois.

Material described above.—Eight specimens: USNM 485944, 485945, interval 5-2, Elwood Formation, Section 5 (Schweizer North), Will County, Illinois; USNM 485946–485951, interval 6-1, Elwood Formation, Section 6 (Plaines West), Will County, Illinois.

Order **AULOPORIDA** Sokolov, 1947

Superfamily **AULOPORICAE** Milne-Edwards and Haime, 1851

Family **AULOPORIDAE** Milne-Edwards and Haime, 1851

Genus **AULOPORA** Goldfuss, 1829

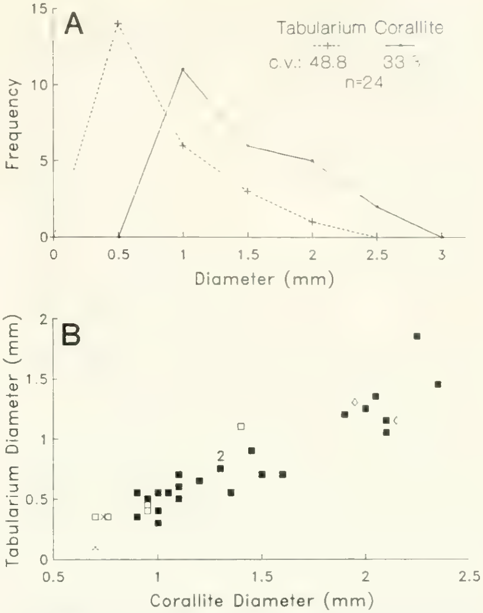
Aulopora Goldfuss, 1829, p. 82.

Type species.—By subsequent designation (Milne-Edwards and Haime, 1850, p. lxxvi): *Aulopora serpens* Goldfuss (1829, p. 82, pl. 29, fig. 1b); Middle Devonian, Bensberg of the Eifel District, Germany.

Diagnosis.—"Corallum reptant, low, commonly adherent; corallites cornute, joined in linear chains or anastomosing; calices slightly raised above substrate, conical or barrel-shaped; walls moderately thick; septal spinules present or absent; tabulae commonly absent, or sparse and oblique; increase basal-lateral; offsets originate on calical surface of wall" (Hill, 1981, p. F631).

Aulopora species A
Plate 20, figures 1–10

Description.—Coralla are reptant in form, umbelliferous in places, and small (Text-fig. 32B). Both of the specimens from Section 23 (Lawrence Quarry) appear to include several small coralla comprising only one or a few corallites. In thin section, corallites are rarely observed to be connected with one another (see Pl. 20, figs. 1, 7, 10); most appear to be immature. In some cases, it is not possible to determine spatial relationships due to extreme variation in orientation of the encrusted substrates. Coralla often encrust other skeletons, including those of *Halysites alexandricus* and calcareous algae (Pl. 20, fig. 1).



Text-figure 32.—Intraspecific variation in *Aulopora* sp. A. **A**, Tabularium and corallite size-frequency distributions; specimen USNM 485785d, Section-interval 23-2 (Lawrence Quarry). n = number of corallites, c.v. = coefficient of variation. **B**, Relationship between tabularium diameter and corallite diameter in specimens from the east-central United States and comparative material of *Aulopora* from Anticosti Island, Québec. Each data point represents a single corallite except as otherwise stated. Symbols for specimens: □ USNM 485780d, Section-interval 23-2 (Lawrence Quarry); n (number of corallites) = 5; ■ USNM 485785d, Section-interval 23-2 (Lawrence Quarry); n = 24 (two corallites plot at the point labelled "2"); ◇ USNM 485952, Section-interval 37-1 (Essex); n = 2; × GSC 111438, Ellis Bay Formation, Anticosti Island, Québec; n = 2.

In transverse section, corallites are subcircular or subovate in shape (Pl. 20, figs. 5, 8, 9). Tabularium and corallite diameters are both variable; the former are 0.30–1.85 mm, the latter 0.70–2.35 mm (Table 20). In longitudinal section, corallites are commonly short; five measured individuals are about 1.6–8.0 mm long. They may be moderately or highly curved, occasionally geniculate (Pl. 20, figs. 2, 10). Basal parts and lower sides of corallites conform to the shapes of their substrates (Pl. 20, figs. 1–4). Corallites generally expanded

Table 20.—Biometric data for *Aulopora* sp. A from the east-central United States. *TaD* = tabularium diameter, *CoD* = corallite diameter, *WT* = wall thickness, *LS* = length of septa; s.d. = standard deviation, c.v. = coefficient of variation.

	parameters			
data	*TaD*	*CoD*	*WT*	*LS*
mean	0.85 mm	1.48 mm	0.312 mm	11%
range of specimen means	0.53–1.22 mm	0.95–2.05 mm	0.185–0.412 mm	0–22%
s.d. of specimen means	0.35 mm	0.55 mm	0.116 mm	16%
c.v. of specimen means	41.2	37.2	37.2	141.4
minimum	0.30 mm	0.70 mm	0.150 mm	—
maximum	1.85 mm	2.35 mm	0.725 mm	—
mean intraspecimen c.v.	54.6	31.4	27.2	—
no. of specimens studied	3	3	3	2

rapidly following initiation; this occurred both in separated, single corallites and in corallites that were produced by offsetting (Pl. 20, figs. 1, 2).

Corallite walls are of variable thickness, thick to very thick, about 0.2–0.4 mm (Table 20). Each wall is composed of two layers. The outer layer is darker, thin or very thin, and appears to have a lamellar structure. The inner layer is paler and thicker, and is concentrically lamellar in transverse section (Pl. 20, fig. 6). In longitudinal section, lamellae of the inner layer may have a wavy appearance (Pl. 20, fig. 3).

Septa are spinose, thorn-like with thickened bases, and slightly upward-directed in longitudinal section (Pl. 20, figs. 3, 6). They are usually sparsely distributed, but may be absent or common in individual corallites (Pl. 20, figs. 2, 5, 7). Septa are usually short, with lengths averaging 11% of tabularium radius (Table 20). Septa are the same color as the lamellar inner wall, and their structure appears to extend from that of the wall. Tabulae are very rare, thin, subhorizontal or slightly convex.

Intraspecific variation.—Although only three specimens are known, there is considerable intraspecific variability in size and in development of skeletal elements (Table 20). A frequency distribution of tabularium and corallite diameters for what appear to be several small coralla in one specimen from Section 23 (Lawrence Quarry) shows a majority of small corallites, with a gradual decrease in numbers with increased size (Text-fig. 32A). This is consistent with the interpretation that most corallites are immature (see also *Aulopora* sp. A, p. 40).

A graph of tabularium diameter *versus* corallite diameter shows that the relationship between these characters is consistent between all specimens (Text-fig. 32B). The specimen from Section 37 (Essex) has corallites that are in the same size range as the larger corallites from Section 23 (Lawrence Quarry). The discontinuity in the data between large and small corallites (Text-fig. 32B) is probably an artifact of the small sample size. There are no obvious differences between specimens or localities in other characters, including corallite shape, wall thickness, and form of septa and tabulae.

Discussion.—As a group, Ordovician and Silurian members of *Aulopora* are poorly understood. In most cases, species have been described only where external surfaces are preserved in three dimensions, with an emphasis on characters such as branching pattern and form of epitheca; internal structures of most are not known (Scrutton, 1990, p. 61). Since auloporids are morphologically extremely simple, this leaves very few points of reference that would permit comparison of those species with thin-sectioned material such as described here. As noted by Webby (1977, p. 175), there has been confusion between *Aulopora* and "gregarious commensal" forms of the family Cornulitidae Fisher, which includes problematic conoidal shells. This confusion was caused by the examination of external surfaces only, since the vesicular wall structure of cornulitids (Fisher, 1962, p. W137, fig. 78) is quite different from the lamellar structure of auloporids. Two of the specimens described above are from the Keel Formation of south-central Oklahoma, a unit in which problematic conoidal shells of the family Tentaculitidae Walcott are also known to occur. The latter are easily distinguished in thin section by their longitudinally striate walls with parallel fibrous structure.

The coralla described above are identified as *Aulopora* sp. A; they are not assigned to a new species because only a few specimens are known and aspects of colony growth are poorly understood. Among other species of comparable age, *Aulopora* sp. A is probably most similar to *Aulopora ellisensis* Twenhofel (1928, p. 124, pl. 2, fig. 14), from the upper part of member 3 of the Ellis Bay Formation on Anticosti Island, Québec (zone 4 of Twenhofel: uppermost Ordovician, Gamachian; Petryk, 1981, fig. 4). We examined the holotype of *A. ellisensis,* which was collected by Twenhofel (YPM 20501). It consists of two corallites exposed in three-dimensions; these are geniculate, rapidly expanding, about 6 to more than 7 mm long, with diameters of about 1 mm, thin walls at the calice rims, and smooth epithecae. Two other auloporid corallites in a specimen from Anticosti that we examined are also similar to *Aulopora* sp. A (GSC 111438; collected by A. A. Petryk in 1983, from a bioherm in member 7 of the Ellis Bay Formation at Point Laframboise). These corallites are smaller than those of *Aulopora* sp. A. They have lamellar walls, thick spinose septa, and the following measured characters: TaD = 0.10–0.35 mm, CoD = 0.70–0.75 mm, WT = 0.20–0.25 mm, LS = 0–50% (compare with Table 20; see Text-fig. 32B).

Two older species have characters similar to those of *Aulopora* sp. A. One is *Aulopora* (?) *trentonensis* Winchell and Schuchert (1895, p. 95, pl. G, figs. 26–28), from the "Trenton Shales" of Minnesota (Decorah Shale according to Bassler, 1950, p. 15), which are of Middle Ordovician, Rocklandian to Shermanian age (Sloan, 1987, fig. 2.6). It has rapidly expanding corallites about 2 mm long and 1 mm in diameter, but these apparently lack septal spines and tabulae. The other species is *Aulopora walliensis* Webby (1977, p. 175, pl. 8, figs. 1–7), from the upper Cliefden Caves Limestone of central-western New South Wales, Australia (Ordovician, Caradoc; Webby *et al.*, 1981, pl. 1). It has corallites with diameters of 1.6–2.2 mm and walls that are 0.2–0.4 mm thick. However, it is distinguished from *Aulopora* sp. A by its parallel, close-spaced, almost fasciculate corallites, and by its apparently specialized mode of life as a commensal on brachiopod shells.

Among younger species that share some characters with *Aulopora* sp. A is *Aulopora* sp. of Bolton (1981a, pl. 10, fig. 7), from the Jupiter Formation of Anticosti Island (lower Lower Silurian, Middle–Upper Llandovery, upper Aeronian–Telychian; Barnes, 1988, fig. 2). *Aulopora* sp. has corallite diameters of about 1.0–1.5 mm and has a reptant growth form, but few other features can be determined. *Aulopora assueta* Klaamann (1966, pp. 66, 67, 93, pl. 21, figs. 4, 5), from the Adavere Stage of Estonia (Upper Llandovery), has thick-walled corallites with diameters up to 2 mm and lengths of 4.5–5.0 mm, that may be reptant or upright. *Aulopora assueta* has weak septa, but it differs from *Aulopora* sp. A in lacking tabulae. *Aulopora enodis* Klaamann (1966, pp. 67, 68, 94, pl. 19, figs. 8, 9, pl. 21, fig. 1), from the Jaagarahu Stage of Estonia (upper Lower Silurian, mid-Wenlock), has a reptant form, corallites that are 4–6 mm long, and short septa, but its corallite diameters of 0.7–1.0 mm are somewhat smaller than is typical of *Aulopora* sp. A.

Occurrences.—Uppermost Ordovician (Gamachian): lower Keel Formation, south-central Oklahoma. Uppermost Ordovician (?; Gamachian?) to lowermost Silurian (Lower Llandovery, lower Rhuddanian): Wilhelmi Formation, northeastern Illinois.

Material described above.—Three specimens: USNM 485780d, 485785d, site 23iv, interval 23-2 (*Brevilamnulella* beds), Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; USNM 485952, interval 37-1, Wilhelmi Formation, Section 37 (Essex), Kankakee County, Illinois.

Order **TETRADIIDA** Okulitch, 1936

Family **TETRADIIDAE** Nicholson, 1879

Genus **RHABDOTETRADIUM** Sokolov, 1955

Rhabdotetradium Sokolov, 1955, p. 247.

Type species.—By original designation: *Rhabdotetradium nobile* Sokolov (1955, p. 248, pl. 57, figs. 1–4); Dolborskaya Horizon (Dolbor Formation: Upper Ordovician, lower Ashgill; Kanygin *et al.*, 1988, pp. 11, 12), Siberian Platform.

Diagnosis.—Tetradiidae with phaceloid coralla. Corallites prismatic to subcircular in outline. Increase quadripartite, corallites diverged after increase. Tabulae rare or absent. (After Hill, 1981, p. F522.)

Remarks.—*Rhabdotetradium* was erected by Sokolov (1955) to include phaceloid tetradiid species; such corals had previously been placed by Bassler (1950, pp. 279–283) in his "*Tetradium syringoporoides* Group." Sokolov's distinction of tetradiid genera has since been disputed by Webby and Semeniuk (1971, pp. 249–251), who argued that growth style was not a valid discriminator, and that *Rhabdotetradium* and the other genera of Sokolov should be considered junior synonyms of *Tetradium* Dana. As Hill (1981, p. F521) pointed out, however, ecophenotypic aspects of tetradiid growth have not been sufficiently investigated. At present, we prefer to maintain the separation of these genera.

Rhabdotetradium species A

Plate 20, figures 11–17

Description of coralla.—All material is fragmentary, so it is not possible to determine larger scale aspects of colony form. Coralla have branching growth forms; each branch is composed of a single corallite except in portions representing corallite increase.

In transverse section, corallites are subcircular to subquadrate or diamond-shaped in outline (Pl. 20, figs. 11–14). They are small, with corallite diameters of 0.40–0.80 mm and tabularium diameters of 0.25–0.65 mm. Walls are moderately thin, 0.05–0.10 mm thick. Walls have a radially fibrous microstructure. Corallites not undergoing increase have four triangulate, apparently laminar septa with slender tips (Pl. 20, figs. 12–14). Lengths of septa are generally about 25% of the corallite radius. Longitudinal sections of corallites cannot be prepared from the available material.

Corallite increase.—Increase was axial, quadripartite, and complete. Prior to division, septa of the parent corallite increased in length to form complete partitions that meet at the axis (Pl. 20, fig. 15). The chambers formed by partitioning developed into four small, subcircular, contiguous, apparently aseptate corallites with corallite diameters of about 0.40–0.45 mm (Pl. 20, fig. 16).

With continued vertical growth, these contiguous corallites developed into separate, broadly divergent, subcircular corallites (Pl. 20, fig. 17). Adjacent individuals with corallite diameters of 0.30–0.40 mm are 0.075 mm apart, and opposite individuals are 0.175 mm apart. At this diameter, corallites possess short, stubby septa with lengths of about 0.05 mm; these septa are oriented so that they point toward the adjacent corallites.

Discussion.—These coralla are identified as *Rhabdotetradium* sp. A; a specific name is not assigned because of the small number and fragmentary nature of specimens. The occurrence of this species in the uppermost Ordovician (Gamachian) of North America is important because it is among the youngest known tetradiids worldwide, and it bears a strong resemblance to some other species of similar age. From the nature and location of the specimens of *Rhabdotetradium* sp. A, it is very unlikely that they were weathered out of older Ordovician rocks and redeposited in the Leemon Formation. Matrix within the calices and between corallites is identical in appearance to common Leemon lithologies, and the corallites are not severely abraded. Tetradiids are not known from the underlying Girardeau Limestone (uppermost Ordovician, Gamachian) and Orchard Creek Shale (Upper Ordovician, Richmondian). From the Blackriveran (Middle Ordovician) Plattin Limestone of Cape Girardeau, Missouri, Bassler (1950, pp. 14, 281) listed *Tetradium syringoporoides* Ulrich (= *Rhabdotetradium syringoporoides*), but that species typically has somewhat larger corallites than does *Rhabdotetradium* sp. A.

The history of tetradiids has been discussed by Webby and Semeniuk (1971, p. 251). Of the species described up to that date, they considered *Rhabdotetradium frutex* Klaamann (1966, pp. 19, 89, fig. 8, pl. 20, figs. 6–8), from the Porkuni Stage of Estonia (uppermost Ordovician, uppermost Ashgill), to be the youngest for which a definite age could be determined. *Rhabdotetradium* sp. A is of about the same age as *R. frutex;* both species have subcircular corallites, but those of the latter are significantly larger (corallite diameters 0.70–1.25 mm). Corallites of *R. frutex* may be separate, like those known from *Rhabdotetradium* sp. A, but they may also be arranged in rows or groups.

Rhabdotetradium sp. A is probably most similar to *Rhabdotetradium nobile* Sokolov (1955, p. 248, pl. 57, figs. 1–4) from the Dolborskaya Horizon of the Siberian Platform (Dolbor Formation: Upper Ordovician, lower Ashgill; Kanygin *et al.*, 1988, pp. 11, 12), also described by Sokolov and Tesakov (1963, p. 97, pl. 21, figs. 6, 7). Like *Rhabdotetradium* sp. A, *R. nobile* has small subcircular to subquadrate corallites with diameters of about 0.5–0.7 mm. In the latter species, however, these are often in contact in groups or short chains.

More recently, *Rhabdotetradium jiangxiense* Lin and Chow, and a subspecies, *R. jiangxiense crassum* Lin and Chow (1977, pp. 158, 159, fig. 12, pl. 39, figs. 1a–1e), have been proposed for material from the Ashgill (undivided) of Chekiang and Kiangsi provinces, China. Both of these have densely spaced subcircular corallites with appearance similar to those of *Rhabdotetradium* sp. A, but they are somewhat larger, with corallite diameters of 0.85–1.50 mm and 0.8–1.3 mm, respectively.

Several older species have corallite diameters similar to those of *Rhabdotetradium* sp. A, but their corallites tend to remain in contact following increase and commonly occur in groups or chains. Such species include: *Tetradium micropora* Bassler (1950, p. 281, pl. 1, figs. 3, 4, pl. 5, figs. 11, 12), from the Lowville Limestone of Tennessee (Blackriveran); *Tetradium oklahomense* Bassler (1950, p. 281, pl. 1, figs. 5, 5′, pl. 5, figs. 13, 13′), from the Bromide Formation of Oklahoma and the Lowville Limestone of Pennsylvania (both Blackriveran); and *Tetradium cribriforme* (Etheridge) as described and illustrated by Webby and Semeniuk (1971, pp. 253–255, pl. 17, figs. 7–12, pl. 18, figs. 1–9) from the lower Cliefden Caves Limestone, Regan's Creek Limestone, mid Bowan Park Limestone (Quondong Limestone of Webby *et al.*, 1981, pl. 1), lower Cargo Creek Limestone, and lower Reedy Creek Limestone of New South Wales, Australia (all Ordovician, Caradoc; Webby *et al.*, 1981, pl. 1).

Occurrence.—Uppermost Ordovician (Gamachian): Leemon Formation, southern Illinois and southeastern Missouri.

Material described above.—Three specimens: USNM 485770b, 485953, interval 31-1, Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois; USNM 423401 (*Rhabdotetradium* sp. A is in matrix enclosing *Streptelasma leemonense*), collected by R. J. Elias and R. J. McAuley in 1983, interval 20-3, Leemon Formation, Section 20 (Short Farm), Cape Girardeau County, Missouri.

Subclass **RUGOSA**
Milne-Edwards and Haime, 1850

Order **STAURIIDA** Verrill, 1865

Suborder **STAURIINA** Verrill, 1865

Family **STAURIIDAE**
Milne-Edwards and Haime, 1850

Genus **PALAEOPHYLLUM** Billings, 1858

Palaeophyllum Billings, 1858, p. 168.

Type species.—By monotypy: *Palaeophyllum rugosum* Billings (1858, p. 168); Ordovician (Blackriveran or Trentonian), Little Discharge, Lac St.-Jean, Québec.

Diagnosis.—"Corallum phacelocerioid or phaceloid, commonly with marginal (lateral) increase; corallites with narrow peripheral stereozone formed by thickening of peripheral ends of septa; short minor septa alternate with long and somewhat wavy major septa that thin rapidly just inside stereozone, then attenuate more slowly as they approach axis, which they reach or almost reach, their axial edges being without paliform lobes; tabulae complete, commonly with axial depression and slightly downturned edges; dissepiments absent; cardinal fossula not distinct" (Hill, 1981, pp. F138, F140).

Palaeophyllum species
Plate 21, figures 1–14

Description.—Growth habits of coralla are fasciculate to cateniform (*i.e.*, with single ranks forming lacunae) or possibly tollinaform (*i.e.*, with multiple ranks and clusters at rank junctions) (Pl. 21, figs. 1–3). Larger scale aspects of colony form cannot be determined because of the fragmentary nature of material.

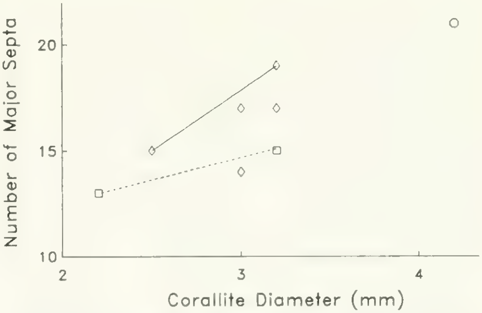
Corallites are cylindrical or subcylindrical, compressed where they come into contact with other individuals (Pl. 21, figs. 1–3, 5). Corallite diameters are 2.2–4.2 mm; most are in the range of 3.0–3.2 mm (Table 21). In longitudinal section, corallites are straight or slightly curved; known lengths are up to 10 mm, but most were probably much longer. Mode of increase is unknown.

Corallite epitheca is very thin; several corallites lack epitheca due to abrasion or corrosion. The outer surface of the epitheca is smooth; septal grooves and interseptal ridges are not seen. The stereozone is narrow to moderately wide. Thickness of the corallite wall is 0.25–0.65 mm, or about 20–30% of the corallite radius (Table 21; Pl. 21, figs. 4, 6, 8, 13). Major septa are long, 80–100% of the corallite radius; 13–21 in number, typically 15–17 (Table 21). Number of major septa is correlated with corallite size (Text-fig. 33). In transverse section, major septa are straight or curved, and may have hooked tips; they usually join together in pairs or in small groups at or near the axis (Pl. 21, figs. 5–8, 10, 11, 13). Thickness of major septa is variable, both within and between corallites; septa may taper axially or have dilated axial ends (Pl. 21, figs. 6, 7). Thickening of all major septa in a corallite tends to be associated with an increased thickness of the stereozone (Pl. 21, fig. 4). Minor septa are thinner and tapered; they are confined to the stereozone or extend beyond it to as much as 20% of the corallite radius (Pl. 21, figs. 5–8, 10, 13).

Table 21.—Biometric data for *Palaeophyllum* sp. from the east-central United States. *CoD* = corallite diameter, *WT* = wall thickness, *NS* = number of major septa, *LS* = length of major septa, *Ta5* = number of tabulae in 5 mm; s.d. = standard deviation, c.v. = coefficient of variation.

	parameters				
data	*CoD*	*WT*	*NS*	*LS*	*Ta5*
mean	3.14 mm	0.34 mm	16.4	89%	4.5
s.d.	0.60 mm	0.12 mm	2.7	6%	—
c.v.	19.1	35.3	16.5	67.4	—
minimum	2.20 mm	0.25 mm	13	80%	4
maximum	4.20 mm	0.65 mm	21	100%	5
no. of corallites studied	7	6	7	7	1

Tabulae are of moderate thickness, highly arched axially, and in some cases are concave upward peripherally (Pl. 21, figs. 9, 12, 14). Tabulae are mostly complete, rarely incomplete. They are moderately widely spaced; spacing at the corallite periphery is about 0.5–



Text-figure 33.—Relationship between number of major septa and corallite diameter in *Palaeophyllum* sp. Each data point represents a transverse thin section of a single corallite; solid line connects sections from different parts of the same corallite; dashed line connects data points for different corallites from a single corallum. Symbols for Section-intervals: □ 23-3 (Lawrence Quarry); n (number of coralla) = 1; ◇ 14-1 and 14-2 (Higginbotham Farm); n = 4; ○ 15-1 (Calumet); n = 1.

1.4 mm, with an average of 4.5 tabulae in 5 mm (Table 21).

Discussion.—These specimens show considerable variability in characters such as septal thickness, axial structure, thickness of stereozone, and growth habit. They may represent more than one species, but since the available specimens are fragmentary and few, it is not possible to make a definite determination. They are identified as *Palaeophyllum* sp.

Several other Late Ordovician and earliest Silurian species of *Palaeophyllum* have cateniform to fasciculate colony growth habits, and corallite diameters and number of major septa comparable to those of *Palaeophyllum* sp. Among these, the most similar is *Palaeophyllum vaurealense* Twenhofel (1928, pp. 122, 123, pl. 4, fig. 1) from the Vauréal Formation of Anticosti Island, Québec (Upper Ordovician, Richmondian; Barnes, 1988, fig. 2), also described and illustrated by Bolton (1979, p. 7, pl. 1.3, figs. 1–10). *Palaeophyllum vaurealense* has corallite diameters of about 2.5–4.4 mm, 13–16 major septa, commonly well-developed minor septa, stereozones of variable thickness, and colony growth habits ranging from sub-cerioid through cateniform to fasciculate. It differs from *Palaeophyllum* sp. by having much more slender major septa that more commonly extend to the corallite axis.

Species of similar character from western North America include: *Palaeophyllum gracile* Flower (1961, pp. 89, 90, pl. 46, pl. 47, figs. 1–8) from the Second Value Formation in Texas (Upper Ordovician, middle Edenian–lowermost Maysvillian; Sweet, 1979, fig. 4), also described and illustrated by Pandolfi (1985, p. 37, pl. 15, fig. 1, pl. 23, figs. 1, 2) from the Upper Ordovician Lost Canyon Member of the Ely Springs Dolomite in the Northern Egan Range, Nevada, and by Gierlowski and Langenheim (1985, p. 7, pl. 1, figs. 1–4) from the Horseshoe Mountain Member of the Bighorn Dolomite in Wyoming (Richmondian); *Palaeophyllum raduguini* Nelson (1963, p. 32, pl. 6, fig. 7) from the Caution Creek and Chasm Creek formations of the Hudson Bay Lowland, northern Manitoba (both Richmondian; see Elias, 1991, fig. 3), also described and illustrated by Bolton (in Bolton and Nowlan, 1979, p. 6, pl. 3, figs. 1, 2, 5) from an outlier north of Aberdeen Lake, Northwest Territories (upper Maysvillian–Richmondian); *Palaeophyllum sinclairi* Caramanica (1992, pp. 75–79, fig. 19, pl. 6, figs. 1–5) from the Bighorn Dolomite in Wyoming (Richmondian); and *Palaeophyllum pasense pasense* Stearn (1956, pp. 89, 90, pl. 16, fig. 7) from the Stonewall Formation in southern Manitoba (uppermost Ordovician to lowermost Silurian, Lower Llandovery, lower Rhuddanian; Sweet, 1979, p. 54, fig. 4; Johnson and Lescinsky, 1986, fig. 2). Our *Palaeophyllum* sp. differs from all of these by having generally thicker major septa, longer minor septa, and thicker stereozones.

Palaeophyllum minimum Yü (1960, pp. 80, 96, pl. 1, figs. 12, 13), from the Upper Ordovician of China, has corallites with diameters of about 3.0–3.5 mm and about 15–19 major septa, but is distinguished from *Palaeophyllum* sp. by having flat tabulae and apparently shorter major septa.

Occurrences.—Uppermost Ordovician (Gamachian): lower Keel Formation, south-central Oklahoma. Lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): Kissenger Limestone Member, Bryant Knob Formation, northeastern Missouri.

Material described above.—Six specimens: USNM 485954, site 23i, interval 23-3, Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; USNM 485955, interval 15-1, Kissenger Limestone Member, Bryant Knob Formation, Section 15 (Calumet), Pike County, Missouri; USNM 485956, interval 14-1, USNM 485957–485959, interval 14-2, Kissenger Limestone Member, Bryant Knob Formation, Section 14 (Higginbotham Farm), Pike County, Missouri.

Family **PYCNOSTYLIDAE** Stumm in Shrock and Twenhofel, 1953

Genus **PYCNOSTYLUS** Whiteaves, 1884

Pycnostylus Whiteaves, 1884, p. 2.

Type species.—By subsequent designation (Miller, 1889, p. 202): *Pycnostylus guelphensis* Whiteaves (1884, pp. 3, 4, pl. 1, figs. 1, 1a, 1b); Guelph Formation (Upper Silurian), Ontario.

Diagnosis.—"Fasciculate, increase peripheral, commonly four offsets simulating axial quadripartite increase; corallites with very narrow peripheral stereozone; septa amplexoid, peripheral continuous part very short; no dissepiments; tabulae complete, horizontal" (Hill, 1981, p. F140).

Pycnostylus species A

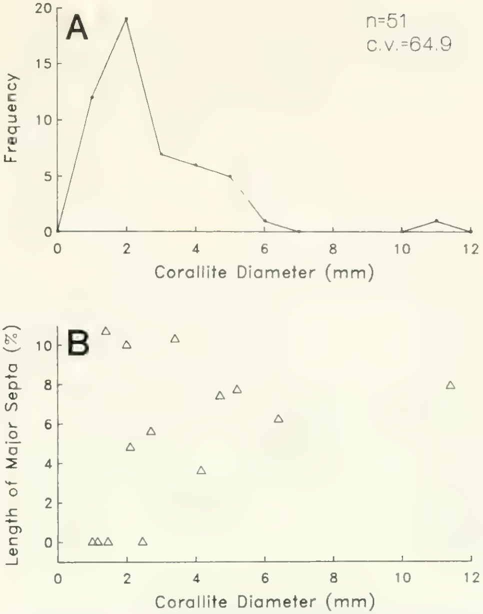
Plate 21, figures 15–25

Description.—All material is fragmentary, so it is not possible to determine larger scale aspects of colony form. Growth habits of coralla are apparently fasciculate.

Corallites are subcylindrical to cylindrical. In transverse section and on external surfaces, they are smooth or have variably developed septal grooves and interseptal ridges (Pl. 21, figs. 16, 17, 23, 25). Corallite diameters are variable, 0.55–11.40 mm but mostly 1–5 mm (Table 22; Text-fig. 34A). Corallites have lengths to more than 35 mm: in longitudinal section they are parallel-sided or slightly conical; walls may be straight

Table 22.—Biometric data for *Pycnostylus* sp. A from the east-central United States. *CoD* = corallite diameter, *WT* = wall thickness, *LS* = length of major septa, *Ta5* = number of tabulae in 5 mm; s.d. = standard deviation, c.v. = coefficient of variation.

	parameters			
data	*CoD*	*WT*	*LS*	*Ta5*
mean	2.76 mm	0.076 mm	5%	2.2
s.d.	1.79 mm	0.027 mm	4%	1.0
c.v.	64.9	35.5	80.3	45.5
minimum	0.55 mm	0.050 mm	0%	1
maximum	11.40 mm	0.175 mm	11%	4
no. of corallites studied	51	41	14	17



Text-figure 34.—Intraspecific variation in *Pycnostylus* sp. A; Section-interval 32-1b (Thomson East). **A**, Corallite size-frequency distribution for all measured corallites; n = number of corallites, c.v. = coefficient of variation. **B**, Relationship between length of major septa as a percentage of corallite radius and corallite diameter, for 14 corallites; each data point represents an individual corallite.

or wavy (Pl. 21, figs. 19, 24). A colonial mode of growth is demonstrated by short to moderately long connections between corallites at or near their bases, which may represent locations of increase (Pl. 21, fig. 20). Connections between more mature parts of corallites are rare or absent.

Corallite walls are thin, 0.050–0.175 mm (Table 22); poor preservation prevents differentiation of the epitheca and stereozone. Septa are lamellar; a single septum can be amplexoid (Pl. 21, figs. 23, 25) or can form a ridge showing relatively constant development (Pl. 21, fig. 18). Major septa are moderately thick and short, with lengths up to 11% of the corallite radius (Table 22). In a transversely sectioned corallite, all major septa are of about the same length (Pl. 21, figs. 16, 23). Minor septa are recognizable where they rarely extend beyond the stereozone. They are short, up to about 3% of the corallite radius, and are thinner than major septa (Pl. 21, fig. 17). Occurrence and abundance of septa generally increase with corallite diameter, with up to 28 major septa in the largest corallites. Septa are absent in all corallites with diameters less than 1 mm; their reduction in transverse sections of some larger individuals (Text-fig. 33B) may be due to the amplexoid nature of septa.

Tabulae are of moderate thickness, commonly concave, convex, or irregular; sometimes incomplete (Pl. 21, figs. 19, 24). They are broadly spaced, averaging about two in 5 mm (Table 22).

Discussion.—These specimens are identified as *Pycnostylus* sp. A. A specific name is not assigned because the material is preserved as dissociated corallites in channel-fill beds, and the degree of breakage prevents assessment of spatial relationships between corallites. This species is the oldest known representative of this Silurian genus, but it is morphologically similar to the other species, which are of early Early Silurian (latest Llandovery) to early Late Silurian (Ludlow) age. *Pycnostylus* sp. A most closely resembles the type species, *Pycnostylus guelphensis* Whiteaves (1884, pp. 3, 4, pl. 1, figs. 1, 1a, 1b), from the Guelph Formation of southwestern Ontario (Ludlow; Winder and Sanford, 1972, fig. 2). The latter species has corallites similar in size to those of *Pycnostylus* sp. A, with diameters of about 3–7 mm, and continuous lamellar septa. Based on Whiteaves' illustrations, it may differ from *Pycnostylus* sp. A by having a higher frequency of corallite increase.

Pycnostylus guelphensis, as described and illustrated by Stearn (1956, p. 82, pl. 8, fig. 7) from the Cedar Lake Formation of southern Manitoba (Upper Llandovery, Telychian, to upper Lower Silurian, Wenlock; Johnson and Lescinsky, 1986, fig. 2), is also very similar to *Pycnostylus* sp. A. Stearn's corals have continuous lamellar or slightly amplexoid septa, occurring in cylindrical corallites that are not joined together above the point of increase. Although the mean corallite diameter given by Stearn (5.6 mm) is significantly larger than that of *Pycnostylus* sp. A, this is apparently based only on corallites that he considered to be mature, and it does fall within the range for our material.

Occurrence.—Lowermost Silurian (Lower Llandovery, lower Rhuddanian): lower Mosalem Formation, northwestern Illinois.

Material described above.—Eight specimens (each includes several dissociated corallites): USNM 485960–485967, interval 32-1b, Mosalem Formation, Section 32 (Thomson East), Carroll County, Illinois.

APPENDIX

STRATIGRAPHIC SECTIONS

Introduction

The locations of stratigraphic sections are designated using United States Geological Survey topographic quadrangle maps (1:24,000 scale). Precise coordinates following the map name are measured in mm first east and then north from the southwest corner of the map. Descriptions of the sections and lists of fossils are contained in the references cited under each entry.

The six outcrop areas (A–F) are outlined in Text-figure 1A (detail map, foldout inside front cover). All the numbered sections (but not Gale Section) were examined during this study. Locations of sections, positions of numbered collection intervals, and stratigraphic and paleontologic data are shown in Text-figures 2–7. Collection intervals are numbered as follows: Section-interval (*e.g.,* 23-2 is Section 23, interval 2).

A. South-central Oklahoma

21 (Rock Crossing).—Overbrook, Oklahoma Quadrangle: 310 mm E, 348 mm N; SE¼ NE¼ SW¼ sec. 35, T 5 S, R 1 E. Exposure on west bank of Hickory Creek, east side of road, 0.15 km south of bridge, Carter County, Oklahoma (Amsden, 1960, sec. Ca11, pp. 208–210, panel 1; Barrick, 1986, sec. Ca11, fig. 39; McAuley and Elias, 1990, sec. 21, pp. 8, 53, fig. 2; Elias, 1992, p. 122, fig. 2). Collection from Section-interval 21-1b made in lens of bioclastic limestone.

22 (Cedar Village).—Turner Falls, Oklahoma Quadrangle: 437 mm E, 326 mm N; SE¼ NE¼ NW¼ sec. 30, T 1 S, R 2 E. Cut on west side of U.S. Route 77, 0.5 km south of junction with Interstate Route 35, just north of Cedar Village, Murray County, Oklahoma (section enlarged and improved since description by Amsden, 1960, sec. M17, pp. 256–258, panel 1; Amsden in Ham, 1973, fig. 35; Barrick, 1986, sec. M17, fig. 39; Fay, 1988, p. 188, fig. 2c; Fay, 1989, marker no. 14, pp. 7, 47, pl. 1; Barrick *et al.,* 1990, p. 5, fig. 2; McAuley and Elias, 1990, sec. 22, pp. 8, 53).

23 (Lawrence Quarry).—Ahloso, Oklahoma Quadrangle. Site 23i: 95 mm E, 301 mm N; NW¼ SE¼ NE¼ sec. 36, T 3 N, R 5 E. Site 23ii: 95 mm E, 290 mm N; SW¼ SE¼ NE¼ sec. 36, T 3 N, R 5 E. Site 23iii: 95 mm E, 288 mm N; SW¼ SE¼ NE¼ sec. 36, T 3 N, R 5 E. Site 23iv: 94 mm E, 286 mm N; NW¼ NE¼ SE¼ sec. 36, T 3 N, R 5 E. East side of Ideal Cement Company quarry at Lawrence, Pontotoc County, Oklahoma; type section of Keel Formation and Ideal Quarry Member (Amsden, 1960, pl. 1, figs. 1, 2, panel 2, pl. A; Amsden, 1974, loc. P22, p. 87; Amsden, 1986, figs. 5, 6, 15; Barrick, 1986, sec. AQL, fig. 39; McAuley and Elias, 1990, sec. 23, pp. 8, 53, fig. 2; Elias, 1992, p. 122, fig. 2).

24 (Coal Creek).—Harden City, Oklahoma Quadrangle: 253 mm E, 208 mm N; NW¼ SE¼ NW¼ sec. 22, T 1 N, R 7 E. Exposure on north bank of Coal Creek, 0.4 km east of Gobbler Knob, Pontotoc County, Oklahoma (Amsden, 1957, fig. 5; Amsden, 1960, sec. P9, pp. 279–282, panel 1; Amsden, 1961, fig. 25; Amsden, 1986, fig. 13; Barrick, 1986, sec. P9, fig. 39; McAuley and Elias, 1990, sec. 24, pp. 8, 53, fig. 2; Elias, 1992, p. 122, fig. 2).

25 (Hunton).—Wapanucka North, Oklahoma Quadrangle: 14 mm E, 519 mm N; NE¼ SE¼ NE¼ sec. 7, T 1 S, R 8 E. Exposure 0.5 km south of northeast corner of section, Coal County, Oklahoma; base of type section of Hunton Group (Amsden, 1960, sec. C1, pp. 182, 184–188, panel 2, pl. B; McAuley and Elias, 1990, sec. 25, p. 53, fig. 2).

35 (Henry House Falls).—Springer, Oklahoma Quadrangle: 65 mm E, 464 mm N; SW¼ NE¼ SE¼ sec. 30, T 2 S, R 1 E. Exposure on west side of Henry House Creek at upper rim of Henry House Falls, Carter County, Oklahoma (Amsden, 1960, sec. Ca1 (2), pp. 190–195, panel 1; Elias, 1992, p. 122, fig. 2).

B. Western north-central Arkansas

33 (Buffalo River).—Marshall, Arkansas Quadrangle: 35 mm E, 512 mm N; NE¼ SW¼ and NW¼ SE¼ sec. 36, T 16 N, R 17 W. Exposure on north bank of Buffalo River, 0.5 km east of bridge on U.S. Route 65, Searcy County, Arkansas (Lemastus, 1979, pp. 86–88, pl. 1; Craig, 1984, p. 11, fig. 2; Craig, 1988, loc. 3, pp. 212, 213, figs. 3, 4; McAuley and Elias, 1990, sec. 33, pp. 10, 53, fig. 3).

C. Southern Illinois and southeastern Missouri

19 (New Wells).—Neelys Landing, Missouri–Illinois Quadrangle: 24 mm E, 254 mm N; NW¼ SW¼ SW¼ sec. 9, T 33 N, R 13 E. Exposure along channel and east bank of Blue Shawnee Creek, 0.5 km east of New Wells, Cape Girardeau County, Missouri (Amsden, 1974, loc. U, pp. 21, 22, 87, fig. 17; Thompson and Satterfield, 1975, sec. 4, p. 79, fig. 9; Elias, 1982, loc. 20b, p. 39, fig. 21; Amsden, 1986, pp. 32–34; McAuley and Elias, 1990, sec. 19, pp. 10, 11, fig. 4).

20 (Short Farm).—Cape Girardeau NE, Missouri Quadrangle: 44 mm E, 276 mm N; SE¼ NE¼ SW¼ sec. 21, T 32 N, R 13 E. Exposure along creek channel just east of barn, 0.25 km east of State Route W, Cape Girardeau County, Missouri; type section of Leemon Formation (Amsden, 1974, loc. K, pp. 19, 85, 86, fig. 16; Thompson and Satterfield, 1975, sec. 3, fig. 7; Elias, 1982, loc. 20a, p. 39, fig. 21; Amsden, 1986, pp. 31, 32, fig. 25; McAuley and Elias, 1990, sec. 20, pp. 10–12, 53, 54, fig. 4). Collections for Section-intervals 20-3 and 20-6 made from loose blocks.

31 (Thebes North).—Thebes, Illinois–Missouri Quadrangle: 157 mm E, 506 mm N; SE¼ SE¼ sec. 5, T 15 S, R 3 W. Exposure on east bank of Mississippi River, 1.5 km southwest of Gale and 1.8 km north of Thebes, Alexander County, Illinois (Savage, 1910, pp. 331, 332, pl. 36, fig. a; Savage, 1913, pp. 20, 21; Savage, 1917, pp. 77–79; Weller, 1940, pp. 8–10; Pryor and Ross, 1962, pp. 7–10, fig. 3; Satterfield, 1971, p. 266, fig. 1; Amsden, 1974, loc. M, pp. 23, 24, 86; Thompson and Satterfield, 1975, sec. 1, pp. 77, 78, fig. 8; Amsden, 1986, pp. 29, 30, fig. 22; McAuley and Elias, 1990, sec. 31, pp. 10–12, 53, fig. 4).

Gale Section.—Thebes, Illinois–Missouri Quadrangle: precise coordinates unknown; NE¼ sec. 4, T 15 S, R 3 W. Abandoned quarry 0.4 km southeast of Gale, Alexander County, Illinois (Savage, 1910, pp. 332, 333, pl. 37, fig. a; Savage, 1913, pp. 21, 22; Savage, 1917, p. 79; McAuley and Elias, 1990, pp. 12, 53, fig. 4) (for cut along State Route 3 in same vicinity, see Weller, 1940, pp. 8–10; Pryor and Ross, 1962, pp. 7–10, fig. 3; Cote *et al.,* 1968, stop 1, pp. 7–10, figs. 6, 7; Amsden, 1974, loc. L, pp. 23, 24, 86; Amsden, 1986, p. 30).

D. West-central Illinois and northeastern Missouri

13 (Bowling Green).—Bowling Green, Missouri Quadrangle: 197 mm E, 497 mm N; NW¼ NW¼ sec. 24, T 53 N, R 3 W. Cut on north side of U.S. Route 54, 1.5 km northeast of junction with U.S. Route 61, Pike County, Missouri; reference section of Cyrene Formation and Bowling Green Dolomite (Koenig *et al.*, 1961, fig. 15; Amsden, 1974, loc. D, p. 84, figs. 4, 7; Thompson and Satterfield, 1975, sec. 8, pp. 96, 99, fig. 11; Elias, 1982, Bowling Green sec., fig. 21; Amsden, 1986, sec. D, figs. 31, 34; McAuley and Elias, 1990, sec. 13, pp. 14, 54, fig. 5; Elias, 1992, p. 122, fig. 3).

14 (Higginbotham Farm).—Cyrene, Missouri Quadrangle: 391 mm E, 418 mm N, and 392 mm E, 424 mm N; W½ NW¼ NE¼ sec. 28, T 53 N, R 1 W. Exposures north (Section-interval 14-1) and south (Section-interval 14-2) of abandoned house (only the foundation remains), just east of State Route D, Pike County, Missouri (Laswell, 1957, sec. 5, p. 20; Amsden, 1974, loc. A, p. 83, fig. 4; Thompson and Satterfield, 1975, p. 93, fig. 16; McAuley and Elias, 1990, sec. 14, p. 54, fig. 5).

15 (Calumet).—Cyrene, Missouri Quadrangle: 415 mm E, 432 mm N, to 404 mm E, 434 mm N; S½ SE¼ sec. 21, T 53 N, R 1 W. Abandoned quarry east of Stark Cemetery, 0.5 km east of State Route D, Pike County, Missouri (Thompson and Satterfield, 1975, sec. 5, p. 93, figs. 15, 16; McAuley and Elias, 1990, sec. 15, p. 54, fig. 5).

16 (Clinton Spring).—Louisiana, Missouri–Illinois Quadrangle: 312 mm E, 312 mm N; SW¼ NE¼ NW¼ sec. 20, T 54 N, R 1 W. Exposure just west of Clinton Spring on west side of State Route 79, southern edge of Louisiana, Pike County, Missouri; type section of Noix Limestone (Laswell, 1957, sec. 4, pp. 18, 19; Koenig *et al.*, 1961, stop 8, p. 34, figs. 21, 22; Birkhead, 1967, loc. I, fig. 4; Amsden, 1974, loc. B, p. 83, fig. 4; Thompson and Satterfield, 1975, sec. 7, p. 89, fig. 12; Elias, 1982, loc. 21b, p. 40, fig. 21; Amsden, 1986, fig. 34, sec. B; McAuley and Elias, 1990, sec. 16, pp. 14, 15, 54, fig. 5).

17 (Clarksville).—Clarksville, Missouri–Illinois and Pleasant Hill West, Illinois–Missouri quadrangles: 333 mm E, 564 mm N (Clarksville) to 313 mm E, 1 mm N (Pleasant Hill West); SW¼ sec. 9, T 53 N, R 1 E. Cut on west side of State Route 79, northern edge of Clarksville, Pike County, Missouri (Amsden, 1974, loc. E, p. 84, figs. 4–6; Thompson and Satterfield, 1975, sec. 6, pp. 99, 100, sec. 6, fig. 13; Elias, 1982, loc. 21a, p. 40; McCracken and Barnes, 1982, fig. 2; Amsden, 1986, sec. E, figs. 33, 34; McAuley and Elias, 1990, sec. 17, pp. 14–16, 54, figs. 5, 6).

18 (Kissenger).—Annada, Missouri–Illinois Quadrangle: 15 mm E, 312 mm N; SW¼ sec. 35 (projected), T 53 N, R 1 E. Cut on west side of State Route 79, just west of Kissenger Hill and south of spring; type section of Bryant Knob Formation and Kissenger Limestone Member (Amsden, 1974, loc. F, pp. 84, 85, fig. 4; Thompson and Satterfield, 1975, sec. 11, pp. 97–100, fig. 14; Amsden, 1986, sec. F, figs. 32, 34; McAuley and Elias, 1990, sec. 18, pp. 14–16, 54, fig. 5).

36 (Indian Creek).—Hamburg, Illinois–Missouri Quadrangle: 183 mm E, 306 mm N; NW¼ NW¼ NE¼ sec. 13, T 10 S, R 3 W. North- and west-facing exposures just south of Indian Creek and just east of County Route 2, 4.6 km south-southeast of Hamburg, Calhoun County, Illinois (Rubey, 1952, loc. 6, pp. 25–27, 170; Amsden, 1974, loc. I, p. 85; Thompson and Satterfield, 1975, sec. 12, p. 106; Elias, 1992, p. 122, fig. 3). Collection for Section-interval 36-2a made from loose block.

E. Northeastern Illinois

3 (Garden Prairie).—Riley, Illinois Quadrangle: 179 mm E, 566 mm N; NE¼ SW¼ sec. 31, T 44 N, R 5 E. Abandoned quarry, 0.5 km south of U.S. Route 20, McHenry County, Illinois (Willman, 1973, pp. 12, 14; McAuley and Elias, 1990, sec. 3, pp. 18, 20, 54, fig. 7).

4 (Schweizer West).—Channahon, Illinois Quadrangle; 302 mm E, 418 mm N; SW¼ SE¼ sec. 35, T 35 N, R 9 E. Cuts on both sides of lower (western) railroad (Section-interval 4-2 on east side of tracks), southeast side of Des Plaines River valley, Will County, Illinois; type section of Wilhelmi Formation, and Schweizer and Birds (lower part) members (Ross, 1962, fig. 1; Willman, 1962, stop 4, p. 84; Willman, 1973, sec. 17, pp. 50, 51; Liebe and Rexroad, 1977, loc. 8, p. 854, fig. 1; Elias, 1982, Will Co. sec., fig. 21; McAuley and Elias, 1990, sec. 4, pp. 18–20, 54, fig. 7; Elias, 1992, p. 123, fig. 4).

5 (Schweizer North).—Channahon, Illinois Quadrangle: 354 mm E, 449 mm N; SW¼ SW¼ NE¼ sec. 36, T 35 N, R 9 E. Cut on southeast side of lower (western) railroad, and ravine from there to southeast side of upper (eastern) railroad, at new concrete culvert, southeast side of Des Plaines River valley, Will County, Illinois; type section of Birds Member (upper part) of Wilhelmi Formation, and Elwood Formation (Ross, 1962, fig. 1; Willman, 1973, sec. 16, p. 50; Liebe and Rexroad, 1977, loc. 7, p. 854, fig. 1; Elias, 1982, Will Co. sec., fig. 21; McAuley and Elias, 1990, sec. 5, pp. 18–20, 54, fig. 7).

6 (Plaines West).—Channahon, Illinois Quadrangle: 405 mm E, 491 mm N; NW¼ SE¼ SW¼ sec. 30, T 35 N, R 10 E. Cut on southeast side of lower (western) railroad, southeast side of Des Plaines River valley, Will County, Illinois; type section of Drummond, Offerman, and Troutman (lower part) members, Kankakee Formation (Ross, 1962, fig. 1; Willman, 1973, sec. 14, pp. 49, 50; Liebe and Rexroad, 1977, loc. 6, p. 854, fig. 1; Elias, 1982, Will Co. sec., fig. 21; McAuley and Elias, 1990, sec. 6, pp. 20, 54, fig. 7).

29 (Sears Pit).—Sycamore, Illinois Quadrangle: 347 mm E, 336 mm N; SE¼ NW¼ and SW¼ NE¼ sec. 15, T 40 N, R 5 E. Quarry southeast of intersection of Barber Greene Road and Airport Road, 4 km northeast of Cortland, De Kalb County, Illinois (Mikulic *et al.*, 1985, pp. 21–23, figs. 6, 7; McAuley and Elias, 1990, sec. 29, pp. 20, 54, fig. 7; Elias, 1992, p. 123, fig. 4). Collection for Section-interval 29-4 made from loose block.

34 (Belvidere South).—Belvidere South, Illinois Quadrangle: 63 mm E, 367 mm N; SE¼ SW¼ NW¼ sec. 14, T 43 N, R 3 E. Abandoned quarry 0.35 km east of Stone Quarry Road, 4 km south of Belvidere, Boone County, Illinois (vicinity of Savage, 1926, p. 518; McAuley and Elias, 1990, sec. 34, pp. 18, 20, 54, fig. 7).

37 (Essex).—Essex, Illinois Quadrangle: 363 mm E, 240 mm N; NW¼ SW¼ SW¼ sec. 12, T 31 N, R 9 E. Exposure on north bank of Horse Creek, 3.3 km east of Essex, Kankakee Co., Illinois (Savage, 1912, p. 100, pl. 7; Savage, 1913, pp. 28, 29; Savage, 1917, pp. 86, 87; Athy, 1928, pp. 38–41, figs. 11, 12; McAuley and Elias, 1990, pp. 18, 20). Collection for Section-interval 37-1 made from loose blocks.

F. Northwestern Illinois and eastern Iowa

8 (King).—Menominee, Illinois–Iowa Quadrangle: 120 mm E, 105 mm N, to 113 mm E, 133 mm N; E½ SE¼ sec. 27, T 88 N, R 3 E. Cut on east side of U.S. Route 52, just south of King, Dubuque County, Iowa; type section of Mosalem and Tete des Morts formations (Willman, 1973, sec. 22, p. 52; McAuley and Elias, 1990, sec. 8, pp. 21, 22, 55).

9 (Winston).—Hanover, Illinois Quadrangle: 41 mm E, 461 mm N; SE¼ SW¼ NE¼ sec. 11, T 27 N, R 1 E. Quarry on east side of road, 1.8 km north of eastern end of Winston railroad tunnel, Jo Daviess County, Illinois (Willman, 1973, sec. 34, p. 55; McAuley and Elias, 1990, sec. 9, pp. 22, 55, fig. 8).

10 (Lost Mound).—Green Island, Iowa–Illinois Quadrangle: 288 mm E, 412 mm N; SW¼ NW¼ SW¼ sec. 28, T 26 N, R 2 E. East side of quarry in east bluff of Mississippi River valley, 1.3 km northwest of Lost Mound, Jo Daviess County, Illinois (Willman, 1973, sec. 24, pp. 52, 53; McAuley and Elias, 1990, sec. 10, pp. 22, 54, fig. 8).

11 (Schapville).—Elizabeth, Illinois Quadrangle: 92 mm E, 558 mm N; NE¼ NE¼ sec. 1, T 27 N, R 2 E. Cut on east side of road, 3.2 km southwest of Schapville, Jo Daviess County, Illinois (Willman, 1973, sec. 30, p. 54; McAuley and Elias, 1990, sec. 11, pp. 22, 55).

12 (Stockton).—Kent, Illinois Quadrangle: 148 mm E, 359 mm N; SE¼ SW¼ SW¼ sec. 17, T 27 N, R 5 E. Abandoned quarry at north edge of ridge, just south of road, 4 km southeast of Stockton, Jo Daviess County, Illinois (Willman, 1973, sec. 32, p. 54; McAuley and Elias, 1990, sec. 12, pp. 22, 55).

26 (Bellevue).—Springbrook, Iowa–Illinois Quadrangle: 288 mm E, 559 mm N, to 262 mm E, 572 mm N; NE¼ sec. 19, T 86 N, R 5 E. Exposure along west side of U.S. Route 52 and south side of road in Bellevue State Park, Jackson County, Iowa (Whitlow and Brown, 1963, p. 13; Ross, 1964, p. 1107, fig. 1; Rose, 1967, stop 3, pp. 44, 45, figs. 20, 21; Anderson, 1983, fig. 5.6; Ludvigson and Witzke, 1988, pp. 236, 237, fig. 21; McAuley and Elias, 1990, sec. 26, pp. 22, 54, 55, fig. 8; Elias, 1992, p. 123, fig. 6).

30 (Thomson Northeast).—Thomson, Illinois Quadrangle: 207 mm E, 452 mm N; NW¼ NW¼ NE¼ sec. 20, T 23 N, R 4 E. Quarry at top of bluff west of Johnson Creek, 3 km northeast of Thomson, Carroll County, Illinois (vicinity of Savage, 1926, p. 527; McAuley and Elias, 1990, sec. 30, pp. 22, 54, fig. 8).

32 (Thomson East).—Thomson, Illinois Quadrangle: 270 mm E, 377 mm N; SE¼ NE¼ NW¼ sec. 28, T 23 N, R 4 E. Quarry on rise east of Johnson Creek, 4.5 km east of Thomson, Carroll County, Illinois (McAuley and Elias, 1990, sec. 32, pp. 22, 54, figs. 8, 9; Elias, 1992, p. 123, fig. 6).

REFERENCES CITED

Aarhus, N.

1982. Lower Silurian tabulate corals of the Oslo region. *in* Field meeting, Oslo region, 1982. D.Worsley, *ed.*, University of Oslo, Paleontological Contributions No. 278, pp. 43–53.

Abbott, B. M.

1974. Flume studies on the stability of model corals as an aid to quantitative palaeoecology. Palaeogeography, Palaeoclimatology, Palaeoecology, vol. 15, pp. 1–27.

Amsden, T. W.

1957. Stratigraphy and paleontology of the Hunton Group in the Arbuckle Mountain region; Part I—Introduction to stratigraphy. Oklahoma Geological Survey, Circular 44, 57 pp.

1960. Stratigraphy and paleontology of the Hunton Group in the Arbuckle Mountain region; Part VI—Hunton stratigraphy. Oklahoma Geological Survey, Bulletin 84, 311 pp.

1961. Stratigraphy of the Frisco and Sallisaw formations (Devonian) of Oklahoma. Oklahoma Geological Survey, Bulletin 90, 121 pp.

1974. Late Ordovician and Early Silurian articulate brachiopods from Oklahoma, southwestern Illinois, and eastern Missouri. Oklahoma Geological Survey, Bulletin 119, 154 pp.

1980. Hunton Group (Late Ordovician, Silurian, and Early Devonian) in the Arkoma Basin of Oklahoma. Oklahoma Geological Survey, Bulletin 129, 136 pp.

1986. Part I; Paleoenvironment of the Keel–Edgewood oolitic province and the Hirnantian strata of Europe, USSR, and China. *in* Late Ordovician–Early Silurian strata in the central United States and the Hirnantian Stage. by T.W.Amsden and J.E.Barrick, Oklahoma Geological Survey, Bulletin 139, pp. 1–55.

1988. Part I; Late Ordovician through Early Devonian annotated correlation chart and brachiopod range charts for the southern midcontinent region, U.S.A. *in* Late Ordovician through Early Devonian annotated correlation chart and brachiopod range charts for the southern midcontinent region, U.S.A., with a discussion of Silurian and Devonian conodont faunas. by T.W.Amsden and J.E.Barrick, Oklahoma Geological Survey, Bulletin 143, pp. 1–53.

Amsden, T. W., and Rowland, T. L.

1965. Silurian stratigraphy of northeastern Oklahoma. Oklahoma Geological Survey, Bulletin 105, 174 pp.

Anderson, W. I.

1983. Geology of Iowa: Over Two Billion Years of Change. Iowa State University, Ames, 268 pp.

Anstey, R. L.

1986. Bryozoan provinces and patterns of generic evolution and extinction in the Late Ordovician of North America. Lethaia, vol. 19, pp. 33–51.

Athy, L. F.

1928. Geology and mineral resources of the Herscher Quadrangle. Illinois State Geological Survey, Bulletin 55, 120 pp.

Bak, R. P. M., and Elgershuizen, J. H. B. W.

1976. Patterns of oil-sediment rejection in corals. Marine Biology, vol. 37, pp. 105–113.

Barnes, C. R.

1988. Stratigraphy and palaeontology of the Ordovician–Silurian boundary interval, Anticosti Island, Quebec, Canada. *in* A global analysis of the Ordovician–Silurian boundary. L.R.M.Cocks and R.B.Rickards, *eds.*, British Museum (Natural History), Bulletin, Geology Series, vol. 43, pp. 195–219.

Barnes, C. R., and Bolton, T. E.

1988. The Ordovician–Silurian boundary on Manitoulin Island, Ontario, Canada, *in* A global analysis of the Ordovician–Silurian boundary. L.R.M.Cocks and R.B.Rickards, *eds.*, British Museum (Natural History), Bulletin, Geology Series, vol. 43, pp. 247–253.

Barnes, C. R., Petryk, A. A., and Bolton, T. E.

1981. Anticosti Island, Québec. *in* Field Meeting, Anticosti–Gaspé, Québec, 1981; vol. 1, Guidebook. P.J.Lespérance, *ed.*, Département de géologie, Université de Montréal, pp. 1–24.

Barrick, J. E.

1986. Part II; Conodont faunas of the Keel and Cason formations. *in* Late Ordovician–Early Silurian strata in the central United States and the Hirnantian Stage. by T.W.Amsden and J.E.Barrick, Oklahoma Geological Survey, Bulletin 139, pp. 57–68.

Barrick, J. E., Klapper, G., and Amsden, T. W.

1990. Stop 1: Hunton Group (Late Ordovician–Early Devonian). *in* Early to middle Paleozoic conodont biostratigraphy of the Arbuckle Mountains, southern Oklahoma. S.M.Ritter, *ed.*, Oklahoma Geological Survey, Guidebook 27, pp. 5–9.

Bassler, R. S.

1950. Faunal lists and descriptions of Paleozoic corals. Geological Society of America, Memoir 44, 315 pp.

Bergström, S. M., and Boucot, A. J.

1988. The Ordovician–Silurian boundary in the United States.

in A global analysis of the Ordovician–Silurian boundary. L.R.M.Cocks and R.B.Rickards, *eds.*, British Museum (Natural History), Bulletin, Geology Series, vol. 43, pp. 273–284.

Berry, W. B. N., and Boucot, A. J.

1970. Correlation of the North American Silurian rocks. Geological Society of America, Special Paper No. 102, 289 pp.

Best, M. B., Boekschoten, G. J., and Oosterbaan, A.

1984. Species concept and ecomorph variation in living and fossil Scleractinia. *in* Recent advances in the paleobiology and geology of the Cnidaria; Proceedings of the Fourth International Symposium on Fossil Cnidaria (and Archaeocyathids and Stromatoporoids) held in Washington, DC, U.S.A., August, 1983. W.A.Oliver, Jr., W.J.Sando, S.D.Cairns, A.G.Coates, I.G.Macintyre, F.M.Bayer, and J.E.Sorauf, *eds.*, Palaeontographica Americana, No. 54, pp. 70–79.

Billings, E.

1858. Report for the year 1857 of E. Billings, Esq., palaeontologist, addressed to Sir W. E. Logan. Geological Survey of Canada, Report of Progress, 1857, pp. 147–192.

1865. Notice of some new genera and species of Palaeozoic fossils. Canadian Naturalist and Geologist, New Series, vol. 2, pp. 425–432.

1866. Catalogues of the Silurian Fossils of the Island of Anticosti, with Descriptions of Some New Genera and Species. Geological Survey of Canada, 99 pp.

Birkhead, P. K.

1967. Stromatoporoidea of Missouri. Bulletins of American Paleontology, vol. 52, No. 234, 110 pp.

Bolton, T. E.

1957. Silurian stratigraphy and palaeontology of the Niagara escarpment in Ontario. Geological Survey of Canada, Memoir 289, 145 pp.

1979. Some Late Ordovician colonial corals from eastern Canada. Geological Survey of Canada, Paper 79-1B, pp. 1–12.

1980. Colonial coral assemblages and associated fossils from the Late Ordovician Honorat Group and White Head Formation, Gaspé Peninsula, Québec. Geological Survey of Canada, Paper 80-1C, pp. 13–28.

1981a. Late Ordovician and Early Silurian Anthozoa of Anticosti Island, Québec. *in* Field Meeting, Anticosti–Gaspé, Québec, 1981; vol. 2, Stratigraphy and Paleontology. P.J.Lespérance, *ed.*, Département de géologie, Université de Montréal, pp. 107–135.

1981b. Early Silurian Anthozoa of Chaleurs Group, Port Daniel–Black Cape region, Gaspé Peninsula, Québec. *in* Field Meeting, Anticosti–Gaspé, Québec, 1981; vol. 2, Stratigraphy and Paleontology. P.J.Lespérance, *ed.*, Département de géologie, Université de Montréal, pp. 299–314.

Bolton, T. E., and Nowlan, G. S.

1979. A Late Ordovician fossil assemblage from an outlier north of Aberdeen Lake, District of Keewatin. Geological Survey of Canada, Bulletin 321, pp. 1–26.

Bondarenko, O. B.

1958. Geliolitidy i tabulyaty ordovika Chu-Iliyskikh gor. Akademiya Nauk SSSR, Geologicheskyi Institut, Trudy, vol. 9, pp. 197–228.

1963. Reviziya roda *Plasmopora*. Paleontolicheskii Zhurnal, 1963, No. 1, pp. 42–52.

1985. Variation and morphogenesis in the Upper Silurian heliolitoids *Paraheliolites* and *Pachyhelioplasma*, from the Podolian Dnestr River region. Paleontological Journal, 1985, No. 2, pp. 18–26.

Bondarenko, O. B., and Minzhin, Ch.

1981. Variation and morphogenesis of the Late Ordovician coral *Propora speciosa*. Paleontological Journal, 1981, No. 1, pp. 6–17.

Brenchley, P. J.

1989. The Late Ordovician extinction. *in* Mass Extinctions: Processes and Evidence. S.K.Donovan, *ed.*, Columbia University Press, pp. 104–132.

Brenchley, P. J., Romano, M., Young, T. P., and Storch, P.

1991. Hirnantian glaciomarine diamictites—evidence for the spread of glaciation and its effect on Upper Ordovician faunas. *in* Advances in Ordovician geology. C.R.Barnes and S.H.Williams, *eds.*, Geological Survey of Canada, Paper 90-9, pp. 325–336.

Brett, C. E., Goodman, W. M., and LoDuca, S. T.

1991. Silurian sequences of the Niagara Peninsula. *in* Sedimentology and Depositional Environments of Silurian Strata of the Niagara Escarpment, Ontario and New York. R.J.Cheel, *ed.*, Geological Association of Canada, Mineralogical Association of Canada, Society of Economic Geologists, Joint Annual Meeting, Toronto '91, Field Trip B4, Guidebook, pp. 3–26.

Brindle, J. E.

1960. The faunas of the lower Palaeozoic carbonate rocks in the subsurface of Saskatchewan. Saskatchewan Department of Mineral Resources, Report No. 52, 45 pp.

Brown, C. E., and Whitlow, J. W.

1960. Geology of the Dubuque South Quadrangle, Iowa–Illinois. United States Geological Survey, Bulletin 1123-A, 93 pp.

Buddemeier, R. W., and Kinzie, R. A., III

1976. Coral growth. Oceanography and Marine Biology: An Annual Review, vol. 14, pp. 183–225.

Buehler, E. J.

1955. The morphology and taxonomy of the Halysitidae. Peabody Museum of Natural History, Bulletin 8, 79 pp.

Caramanica, F. P.

1992. Ordovician corals of the Red River–Stony Mountain Province. *in* Proceedings of the F. D. Holland, Jr., geological symposium. J.M.Erickson and J.W.Hoganson, *eds.*, North Dakota Geological Survey, Miscellaneous Series 76, pp. 23–97.

Chernyshev, B. B.

1937. Verkhnesiluriyskie i devonskie Tabulata Novoy Zemli, Severnoy Zemli, i Taymyra. Vsesoiuznoe Arktiki Institut, Trudy, vol. 91, pp. 67–134.

1941. Siluriyskie i nizhnedevonskie korally basseyna reki Tarei (yugo-zapadnyy Taymyr). Vsesoiuznoe Arktiki Istitut, Trudy, vol. 158, No. 5, pp. 9–64.

Coates, A. G.

1984. Taxonomic methods in living corals and their paleontologic implications: Introduction. *in* Recent advances in the paleobiology and geology of the Cnidaria; Proceedings of the Fourth International Symposium on Fossil Cnidaria (and Archaeocyathids and Stromatoporoids) held in Washington, DC, U.S.A., August, 1983. W.A.Oliver, Jr., W.J.Sando, S.D.Cairns, A.G.Coates, I.G.Macintyre, F.M.Bayer, and J.E.Sorauf, *eds.*, Palaeontographica Americana, No. 54, pp. 15–17.

Copper, P.

1978. Paleoenvironments and paleocommunities in the Ordovician–Silurian sequence of Manitoulin Island. Michigan

Basin Geological Society, Special Papers No. 3, pp. 47–61.

Cote, W., Reinertsen, D., and Killey, M.

1968. Guide Leaflet, Geological Science Field Trip, Thebes Area, Alexander County, Jonesboro and Thebes Quadrangles. Illinois State Geological Survey, 32 pp.

Craig, W. W.

1984. Silurian stratigraphy of the Arkansas Ozarks. *in* Contributions to the geology of Arkansas, vol. 2. J.D.McFarland, III and W.V.Bush, *eds.*, Arkansas Geological Commission, Miscellaneous Publication 18B, pp. 5–32.

1988. Geology of the Buffalo River valley in the vicinity of U.S. 65, Arkansas Ozarks, *in* South-Central Section of the Geological Society of America. O.T.Hayward, *ed.*, Geological Society of America, Centennial Field Guide, vol. 4, pp. 211–214.

Dana, J. D.

1846. Structure and Classification of Zoophytes: U.S. Exploring Expedition During the Years 1838, 1839, 1840, 1841, 1842 Under the Command of Charles Wilkes, U.S.N.; vol. 7. Lea and Blanchard, Philadelphia, 740 pp.

Dixon, J.

1976. Corallite increase and a new corallite type in Upper Ordovician cateniform corals. Journal of Paleontology, vol. 50, pp. 916–921.

Dixon, O. A.

1974. Late Ordovician *Propora* (Coelenterata: Heliolitidae) from Anticosti Island, Quebec, Canada. Journal of Paleontology, vol. 48, pp. 568–585.

1986. The heliolitid coral *Acidolites* in Ordovician–Silurian rocks of eastern Canada. Journal of Paleontology, vol. 60, pp. 26–52.

Eckert, J. D.

1988. Late Ordovician extinction of North American and British crinoids. Lethaia, vol. 21, pp. 147–167.

Ehrenberg, C. G.

1834. Beiträge zur physiologischen Kenntniss der Corallenthiere im allgemeinen, und besonders des Rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. Akademie der Wissenschaften, physikalisch-mathematische Klasse, Abhandlungen (1832), pp. 225–380.

Eichwald, E. d'

1855–1860. Lethaea Rossica ou paléontologie de la Russie: vol. 1, Part 1. E. Schweizerbart, Stuttgart, pp. xix + 17–26 + 1–681 (atlas, 1855; text, 1860).

Elias, R. J.

1982. Latest Ordovician solitary rugose corals of eastern North America. Bulletins of American Paleontology, vol. 81, No. 314, 116 pp.

1989. Extinctions and origins of solitary rugose corals, latest Ordovician to earliest Silurian in North America. *in* Fossil Cnidaria 5; Proceedings of the Fifth International Symposium on Fossil Cnidaria Including Archaeocyatha and Spongiomorphs held in Brisbane, Queensland, Australia, 25–29 July 1988. P.A.Jell and J.W.Pickett, *eds.*, Association of Australasian Palaeontologists, Memoir 8, pp. 319–326.

1991. Environmental cycles and bioevents in the Upper Ordovician Red River–Stony Mountain solitary rugose coral province of North America. *in* Advances in Ordovician geology. C.R.Barnes and S.H.Williams, *eds.*, Geological Survey of Canada, Paper 90-9, pp. 205–211.

1992. New information on latest Ordovician to earliest Silurian solitary rugose corals of the east-central United States. *in* Special papers in paleontology and stratigraphy: a tribute to Thomas W. Amsden. J.R.Chaplin and J.E.Barrick, *eds.*, Oklahoma Geological Survey, Bulletin 45, pp. 113–125.

Elias, R. J., and Young, G. A.

1992. Biostratigraphy and biogeographic affinities of latest Ordovician to earliest Silurian corals in the east-central United States. *in* Global Perspectives on Ordovician Geology. Proceedings of the Sixth International Symposium on the Ordovician System, University of Sydney, Australia, 15–19 July 1991. B.D.Webby and J.R.Laurie, *eds.*, A. A. Balkema, Rotterdam, pp. 205–214.

Elias, R. J., Zeilstra, R. G., and Bayer, T. N.

1988. Paleoenvironmental reconstruction based on horn corals, with an example from the Late Ordovician of North America. Palaios, vol. 3, pp. 22–34.

Fay, R. O.

1988. I-35 roadcuts. Geology of Paleozoic strata in the Arbuckle Mountains of southern Oklahoma. *in* South-Central Section of the Geological Society of America. Geological Society of America, Centennial Field Guide. O.T.Hayward, *ed.*, vol. 4., pp. 183–188.

1989. Geology of the Arbuckle Mountains along Interstate 35, Carter and Murray Counties, Oklahoma. Oklahoma Geological Survey, Guidebook 26, 50 pp.

Fischer-Benzon, R. von

1871. Mikroskopische Untersuchungen über die Structur der Halysites-Arten und einiger silurischer Gesteine aus den russischen Ostsee-Provinzen. Abhandlungen aus dem Gebeite der Naturwissenschaften Verein Hamburg, vol. 5, sec. 2, 31 pp.

Fischer von Waldheim, G. F.

1813. Zoognosia tabulis synopticis illustrata . . . ; Edition 3, vol. 1. Nicolai S. Vsevolzsky, Moscow, 465 pp.

1828. Notice sur les polypiers tubipores fossiles. Université Impériale (Moscow), pp. 9–23.

Fisher, D. W.

1962. Small conoidal shells of uncertain affinities. *in* Treatise on Invertebrate Paleontology. R.C.Moore, *ed.*, Part W, Miscellanea. Geological Society of America and University of Kansas Press, pp. W98–W143.

Flower, R. H.

1961. Montoya and related colonial corals. Mew Mexico Bureau of Mines and Mineral Resources, Memoir 7, Part I, pp. 1–97.

Flower, R. H., and Duncan, H. M.

1975. Some problems in coral phylogeny and classification. *in* Studies in paleontology and stratigraphy. J.Pojeta, Jr. and J.K.Pope, *eds.*, Bulletins of American Paleontology, vol. 67, No. 287, pp. 175–192.

Foerste, A. F.

1909. Fossils from the Silurian formations of Tennessee, Indiana, and Illinois. Denison University, Scientific Laboratories, Bulletin, vol. 14, pp. 61-116.

Foster, A. B.

1985. Variation within coral colonies and its importance for interpreting fossil species. Journal of Paleontology, vol. 59, pp. 1359–1381.

Frech, F.

1897. Referat, J. Wentzel: Zur Kenntniss der Zoantharia tabulata. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, 1897 (Part 2), pp. 212–214.

Fritz, M. A.

1937. *Multisolenia,* a new genus of Paleozoic corals. Journal of Paleontology, vol. 11, pp. 231–234.

Gibson, M. A., and Broadhead, T. W.

1989. Species-specific growth responses of favositid corals to soft-bottom substrates. Lethaia, vol. 22, pp. 287–299.

Gierlowski, T. C., and Langenheim, R. L., Jr.

1985. Corals from the Late Ordovician Horseshoe Mountain Member, Bighorn Dolomite, Bighorn Mountains, Sheridan County, Wyoming. Wyoming Geological Association, Earth Science Bulletin, vol. 18, pp. 1–21.

Girty, G. H.

1895. Development of the corallum in *Favosites forbesi,* var. occidentalis. American Geologist, vol. 15, pp. 131–146.

Goldfuss, G. A.

1829. Petrefacta Germaniae, I. Arnz and Co., Düsseldorf, pp. 77–164.

Hall, J.

1847. Natural History of New York, Part 6: Palaeontology of New York, vol. 1. C. van Benthuysen, Albany, 338 pp.

Hall, R. L.

1975. Late Ordovician coral faunas from north-eastern New South Wales. Royal Society of New South Wales, Journal and Proceedings, vol. 108, pp. 75–93.

Ham, W. E.

1973. Regional geology of the Arbuckle Mountains, Oklahoma. Oklahoma Geological Survey, Special Publication 73-3, 61 pp.

Hamada, T.

1957. On the classification of the Halysitidae, I. University of Tokyo, Faculty of Science, Journal, sec. 2, vol. 10, Part 3, pp. 393–405.

1959. Corallum growth of the Halysitidae. University of Tokyo, Faculty of Science, Journal, sec. 2, vol. 11, Part 3, pp. 273–289.

Harrington, R. J.

1987. Lithofacies and biofacies of the Middle and Upper Devonian Sultan Formation at Mountain Springs, Clark County, Nevada: implications for stromatoporoid paleoecology. Journal of Paleontology, vol. 61, pp. 649–662.

Hill, D.

1959. Some Ordovician corals from New Mexico, Arizona, and Texas. New Mexico Bureau of Mines and Mineral Resources, Bulletin 64, 25 pp.

1981. Supplement 1: Rugosa and Tabulata. 2 vols. *in* Treatise on Invertebrate Paleontology. C.Teichert, *ed.*, Part F, Coelenterata. Geological Society of America and University of Kansas, 762 pp.

Hill, D., and Stumm, E. C.

1956. Tabulata. *in* Treatise on Invertebrate Paleontology. R.C.Moore, *ed.*, Part F, Coelenterata. Geological Society of America and University of Kansas Press, pp. F444–F477.

Hodges, L. T., and Roth, A. A.

1986. Orientation of corals and stromatoporoids in some Pleistocene, Devonian, and Silurian reef facies. Journal of Paleontology, vol. 60, pp. 1147–1158.

Hubbard, J. A. E. B., and Pocock, Y. P.

1972. Sediment rejection by Recent scleractinian corals: a key to palaeo-environmental reconstruction. Geologischen Rundschau, vol. 61, pp. 598–626.

Hubmann, B.

1992. Variabilitätsuntersuchungen an *Catenipora* Lamarck (Zoantharia, Tabulata). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, vol. 5, pp. 279–291.

Hunter, C. L.

1985. Assessment of clonal diversity and population structure of *Porites compressa* (Cnidaria, Scleractinia). *in* Proceedings of the Fifth International Coral Reef Congress, Tahiti, 27 May–1 June 1985, vol. 6, Miscellaneous Papers (B). Antenne Museum-Ephe, pp. 69–74.

Ivanov, A. N.

1950. Descriptions. *in* Opredelitel fauny Ordovika zapadnogo sklona Srednego Urala. by A.N.Ivanov and E.I.Myagkova, Akademiya Nauk SSR, Uralskii Filial, Gorno-Geologicheskogo Instituta, Trudy, 18, pp. 1–31.

Jaanusson, V.

1963. Classification of the Harjuan (Upper Ordovician) rocks of the mainland of Sweden. Geologiska Föreningens i Stockholm Förhandlingar, vol. 85, pp. 110–144.

Jaanusson, V., and Mutvei, H.

1982. Ordovician of öland: Guide to Excursion 3, IV International Symposium on the Ordovician System. Swedish Museum of Natural History, Section of Palaeozoology, 23 pp.

Jackson, J. B. C.

1983. Biological determinants of present and past sessile animal distributions. *in* Biotic Interactions in Recent and Fossil Benthic Communities. M.J.S.Tevesz and P.L.McCall, *eds.*, Plenum Press, New York, pp. 39–120.

Johnson, M. E., and Lescinsky, H. L.

1986. Depositional dynamics of cyclic carbonates from the Interlake Group (Lower Silurian) of the Williston Basin. Palaios, vol. 1, pp. 111–121.

Johnson, M. E., Rong Jia-yu, and Yang Xue-chang

1985. Intercontinental correlation by sea-level events in the Early Silurian of North America and China (Yangtze Platform). Geological Society of America, Bulletin, vol. 96, pp. 1384–1397.

Jones, O. A.

1936. The controlling effect of environment upon the corallum in *Favosites*; with a revision of some massive species on this basis. Annals and Magazine of Natural History, Series 10, vol. 17, pp. 1–24.

Kaljo, D., Nestor, H., and Paalma, L.

1988. East Baltic region. *in* A global analysis of the Ordovician–Silurian boundary. L.R.M.Cocks and R.B.Rickards, *eds.*, British Museum (Natural History), Bulletin, Geology Series, vol. 43, pp. 85–91.

Kanygin, A. V., Moskalenko, T. A., and Yadrenkina, A. G.

1988. The Siberian platform. *in* The Ordovician System in most of Russian Asia; correlation charts and explanatory notes. R.J.Ross, Jr. and J.A.Talent, *eds.*, International Union of Geological Sciences, Publication No. 26, pp. 1–27.

Kershaw, S.

1984. Patterns of stromatoporoid growth in level-bottom environments. Palaeontology, vol. 27, pp. 113–130.

1990. Stromatoporoid palaeobiology and taphonomy in a Silurian biostrome in Gotland, Sweden. Palaeontology, vol. 33, pp. 681–705.

Kiaer, J.

1899. Die Korallenfaunen der Etage 5 des norwegischen Silursystems. Palaeontographica, vol. 46, pp. 1–60.

1930. Den fossilførende ordovicisk–siluriske lagrekke på Stord, og bemerkninger om de øvrige fossilfunn i Bergensfeltet. Bergens Museums Årbok 1929, Naturvidenskapelig rekke, No. 11, 75 pp.

Klaamann, E. R.

1959. O faune tabulyat yuuruskogo i tamsaluskogo gorizontov. Eesti NSV Teaduste Akadeemia Toimetised, vol. 8, Tehniliste ja Füüsikalis-Matemaatiliste Teaduste, Series No. 4, pp. 256–270.

1961. Tabulyaty i geliolitidy Venlocka Estonii. Eesti NSV Teaduste Akadeemia, Geoloogia Instituut, Uurimused, vol. 6, pp. 69–112.

1962. Tabulyaty verkhnego Silura Estonii. Eesti NSV Teaduste Akadeemia, Geoloogia Instituut, Uurimused, vol. 9, pp. 25–74.

1964. Pozdneordovikskie i rannesiluriyskie Favositida Estonii. Eesti NSV Teaduste Akadeemia, Geoloogia Instituut, 118 pp.

1966. Inkommunikatnye tabulyaty Estonii. Eesti NSV Teaduste Akadeemia, Geoloogia Instituut, 96 pp.

Kobluk, D. R., Bottjer, D. J., and Risk, M. J.

1977. Disorientation of Paleozoic hemispherical corals and stromatoporoids. Canadian Journal of Earth Sciences, vol. 14, pp. 2226–2231.

Koenig, J. W., Martin, J. A., and Collinson, C. W.

1961. Guidebook, twenty-sixth regional field conference, the Kansas Geological Society, northeastern Missouri and west-central Illinois. Missouri Division of Geological Survey and Water Resources, Report of Investigations, No. 27, 168 pp.

Lafuste, J., and Tourneur, F.

1988. Microstructure du genre *Favosites* Lamarck 1816 (Tabulata) et de favositidés du Silurien, avec une revision du neotype de *Favosites gothlandicus* Lamarck 1816. Annales de la Société géologique de Belgique, vol. 110-1987, pp. 189–198.

Lamarck, J. B. P. A. de M. de

1816. Histoire naturelle des animaux sans vertèbres; vol. 2. The author, Paris, 568 pp.

Lambe, L. M.

1899. A revision of the genera and species of Canadian Palaeozoic corals; the Madreporaria Perforata and the Alcyonaria. Geological Survey of Canada, Contributions to Canadian Palaeontology, vol. 4, Part 1, pp. 1–96.

Lang, W. D., Smith, S., and Thomas, H. D.

1940. Index of Palaeozoic Coral Genera. British Museum (Natural History), 231 pp.

Lasker, H. R.

1980. Sediment rejection by reef corals: the roles of behavior and morphology in *Montastrea cavernosa* (Linnaeus). Journal of Experimental Marine Biology and Ecology, vol. 47, pp. 77–87.

Laswell, T. J.

1957. Geology of the Bowling Green Quadrangle, Missouri. Missouri Division of Geological Survey and Water Resources, Report of Investigations, No. 22, 64 pp.

Laub, R. S.

1979. The corals of the Brassfield Formation (mid-Llandovery; Lower Silurian) in the Cincinnati Arch region. Bulletins of American Paleontology, vol. 75, No. 305, 457 pp.

Laufeld, S., and Jeppsson, L.

1976. Silicification and bentonites in the Silurian of Gotland. Geologiska Föreningens i Stockholm Förhandlingar, vol. 98, pp. 31–44.

Lee, D.-J., and Elias, R. J.

1991. Mode of growth and life-history strategies of a Late Ordovician halysitid coral. Journal of Paleontology, vol. 65, pp. 191–199.

Lee, D.-J., and Noble, J. P. A.

1988. Evaluation of corallite size as a criterion for species discrimination in favositids. Journal of Paleontology, vol. 62, pp. 32–40.

1990. Reproduction and life strategies in the Paleozoic tabulate coral *Paleofavosites capax* (Billings). Lethaia, vol. 23, pp. 257–272.

Leleshus, V. L.

1974. Novye pozdnesiluriyskie geliolitoidei yuzhnogo Tyan-Shanya. Akademiya Nauk Tadzhikistana SSR, Izvestia, Otdelstvo Fiziko-Matematicheskikh i Geologo-Khimicheskikh Nauk, vol. 4, pp. 94–101.

Lemastus, S. W.

1979. Stratigraphy of the Cason Shale (Ordovician–Silurian), Northern Arkansas. University of New Orleans, New Orleans, Louisiana, M.Sc. thesis, 93 pp.

Lespérance, P. J., Malo, M., Sheehan, P. M., and Skidmore, W. B.

1987. A stratigraphical and faunal revision of the Ordovician–Silurian strata of the Percé area, Quebec. Canadian Journal of Earth Sciences, vol. 24, pp. 117–134.

Liebe, R. M., and Rexroad, C. B.

1977. Conodonts from Alexandrian and early Niagaran rocks in the Joliet, Illinois, area. Journal of Paleontology, vol. 51, pp. 844–857.

Lin Baoyu

1965. Ordovician corals from the provinces of Kweichow and Szechuan and their stratigraphical significance [Chinese with Russian summary]. Acta Palaeontologica Sinica, vol. 13, pp. 64–93.

Lin Baoyu and Chow Xing-hu

1977. Tabulata and Heliolitida of the Upper Ordovician of the Chekiang and Kiangsi provinces and their stratigraphical significance [in Chinese]. Professional Papers of Stratigraphy and Palaeontology, No. 3, pp. 108–208.

Lindström, G.

1899. Remarks on the Heliolitidae. Kongliga Svenska Vetenskaps-Akademiens Handlingar, vol. 32, No. 1, 140 pp.

Linnaeus, C.

1767. Systema naturae . . . ; Edition 12, vol. 1, Part 2. Laurentius Salvius, Holmiae, pp. 533–1327 + (37).

Lonsdale, W.

1839. Corals, graptolites, and nondescripts. *in* The Silurian System Founded on Geological Researches in the Counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester, and Stafford, with Descriptions of the Coal-Fields and Overlying Formations. by R.I. Murchison, vols. 1, 2. John Murray, London, pp. 675–698.

Ludvigson, G. A., and Witzke, B. J.

1988. Sunday, Stop 1: Exposures of the Silurian–Ordovician contact at Bellevue State Park; the Mosalem, Tete des Morts, and Blanding formations. *in* New perspectives on the Paleozoic history of the Upper Mississippi Valley: an examination of the Plum River Fault Zone. G.A.Ludvigson and B.J.Bunker, *eds.*, Iowa Department of Natural Resources, Guidebook No. 8, pp. 234–238.

Maher, J. C., and Lantz, R. J.

1952. Described sections and correlation of Paleozoic rocks at Gilbert, Carver, and Marshall, Arkansas. United States Geological Survey, Circular 160, 21 pp.

Manten, A. A.

1971. Silurian Reefs of Gotland (Developments in Sedimentology 13). Elsevier, Amsterdam, 539 pp.

Maxwell, R. A.

1936. The Stratigraphy and Areal Distribution of the "Hunton Formation", Oklahoma. unpublished PhD thesis, Northwestern University, Evanston, 120 pp.

McAuley, R. J., and Elias, R. J.

1990. Latest Ordovician to earliest Silurian solitary rugose corals of the east-central United States. Bulletins of American Paleontology, vol. 98, No. 333, 82 pp.

McCracken, A. D., and Barnes, C. R.

1982. Restudy of conodonts (Late Ordovician–Early Silurian) from the Edgewood Group, Clarksville, Missouri. Canadian Journal of Earth Sciences, vol. 19, pp. 1474–1485.

Melchin, M. J., McCracken, A. D., and Oliff, F. J.

1991. The Ordovician–Silurian boundary on Cornwallis and Truro islands, Arctic Canada: preliminary data. Canadian Journal of Earth Sciences, vol. 28, pp. 1854–1862.

Mikulic, D. G., Sargent, M. L., Norby, R. D., and Kolata, D. R.

1985. Silurian geology of the Des Plaines River valley, northeastern Illinois. Illinois State Geological Survey, Guidebook 17, 56 pp.

Miller, S. A.

1889. North American Geology and Palaeontology for the Use of Amateurs, Students, and Scientists. Western Methodist Book Concern, Cincinnati, 664 pp.

Milne-Edwards, H., and Haime, J.

1849. Mémoire sur les polypiers appartenant aux groupes naturels des Zoanthaires perforés et des Zoanthaires tabulés. Académie des Sciences de Paris, Comptes Rendus, vol. 29, pp. 257–263.

1850. A Monograph of the British Fossil Corals: Introduction. Palaeontographical Society, vol. 3, pp. i–lxxxv.

1851. Monographie des polypiers fossiles des terrains palaeozoïques, précédée d'un tableau général de la classification des polypes. Muséum d'Histoire Naturelle, Paris, Archives, vol. 5, 502 pp.

Mironova, N. V.

1960. Dva novykh roda tabulyat. Sibirskogo Nauchno-Issledovatelskogo Instituta Geologii, Geofiziki i Mineralnogo Syrya (SNIIGGIMS), Trudy, vol. 8, pp. 95–98.

Nelson, S. J.

1963. Ordovician paleontology of the northern Hudson Bay Lowland. Geological Society of America, Memoir 90, 152 pp.

Nicholson, H. A.

1879. On the Structure and Affinities of the "Tabulate Corals" of the Palaeozoic Period. William Blackwood and Sons, Edinburgh, 342 pp.

Nicholson, H. A., and Etheridge, R., Jr.

1878. A Monograph of the Silurian Fossils of the Girvan District in Ayrshire; vol. 1, No. 1. William Blackwood and Sons, Edinburgh, pp. 1–135.

1880. A Monograph of the Silurian Fossils of the Girvan District in Ayrshire; vol. 1, No. 3. William Blackwood and Sons, Edinburgh, pp. 237–341.

Noble, J. P. A., and Young, G. A.

1984. The Llandovery–Wenlock heliolitid corals from New Brunswick, Canada. Journal of Paleontology, vol. 58, pp. 867–884.

Northrop, S. A.

1939. Paleontology and stratigraphy of the Silurian rocks of the Port Daniel–Black Cape region, Gaspé. Geological Society of America, Special Paper 21, 302 pp.

Nowlan, G. S.

1983. Early Silurian conodonts of eastern Canada. Fossils and Strata, No. 15, pp. 95–110.

Nutting, C. C.

1900. American hydroids; Part I: The Plumularidae. U.S. National Museum, Special Bulletin, vol. 4, pp. 1–285.

Oekentorp, K.

1971. *Palaeofavosites* Twenhofel, 1914 (Anthozoa, Tabulata): proposed validation under the plenary powers. Z.N.(S.) 1961. Bulletin of Zoological Nomenclature, vol. 28, Part 5/6, pp. 158–160.

1976. Revision und Typisierung des Genus *Paleofavosites* Twenhofel, 1914. Paläontologische Zeitschrift, vol. 50, No. 3/4, pp. 151–192.

Oekentorp, K., and Schouppé, A. von

1969. Kritische Betrachtungen über die Anordnung der Poren bei *Palaeofavosites* Twenhofel, 1914. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, vol. 133, pp. 89–100.

Okulitch, V. J.

1936. On the genera *Heliolites, Tetradium*, and *Chaetetes*. American Journal of Science, vol. 32, pp. 361–379.

Oliver, W. A., Jr.

1968. Some aspects of colony development in corals. *in* Paleobiological aspects of growth and development, a symposium. D.B.Macurda, Jr., *ed.*, Paleontological Society, Memoir 2 (Journal of Paleontology, vol. 42, No. 5, supplement), pp. 16–34.

Orbigny, A. d'

1850. Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés; vol. 1. Victor Masson, Paris, 349 pp.

Owen, D. D.

1844. Report of a geological exploration of part of Iowa, Wisconsin, and Illinois, made under instructions from the Secretary of the Treasury of the United States, in the autumn of the year 1839. 28th Congress, First Session, [Senate], [407], 191 pp.

Owen, A. W., Bruton, D. L., Bockelie, J. F., and Bockelie, T. G.

1990. The Ordovician successions of the Oslo region, Norway. Norges Geologiske Undersøkelse, Special Publication No. 4, 54 pp.

Ozaki, K.

1934. Description of fossils, A: Corals, pp. 62–78 *in* Shimizu, S., Ozaki, K., and Obata, T., *Gotlandian deposits of northwest Korea*. Shanghai Science Institute, Journal, sec. 2, vol. 1, pp. 59–88.

Pandolfi, J. M.

1984. Environmental influence on growth form in some massive tabulate corals from the Hamilton Group (Middle Devonian) of New York State. *in* Recent advances in the paleobiology and geology of the Cnidaria; Proceedings of the Fourth International Symposium on Fossil Cnidaria (and Archaeocyathids and Stromatoporoids) held in Washington, DC, U.S.A., August, 1983. W.A.Oliver, Jr., W.J.Sando, S.D.Cairns, A.G.Coates, I.G.Macintyre, F.M.Bayer, and J.E.Sorauf, *eds.*, Palaeontographica Americana, No. 54, pp. 538–542.

1985. Late Ordovician and Silurian of the Eastern Great Basin, part 5: colonial corals from the Ely Springs Dolomite. Milwaukee Public Museum, Contributions in Biology and Geology, No. 61, 95 pp.

Petryk, A. A.

1981. Stratigraphy, sedimentology and paleogeography of the Upper Ordovician–Lower Silurian of Anticosti Island, Québec. *in* Field Meeting, Anticosti–Gaspé, Québec, 1981; vol. 2, Stratigraphy and Paleontology. P.J.Lespérance, *ed.*, Département de géologie, Université de Montréal, pp. 11–39.

Philcox, M. E.

1971. Growth forms and role of colonial coelenterates in reefs of the Gower Formation (Silurian), Iowa. Journal of Paleontology, vol. 45, pp. 338–346.

Philip, G. M.

1960. The Middle Palaeozoic squamulate favositids of Victoria. Palaeontology, vol. 3, pp. 186–207.

Pickerill, R. K., and Harland, T. L.

1984. Middle Ordovician microborings of probable sponge origin from eastern Canada and southern Norway. Journal of Paleontology, vol. 58, pp. 885–891.

Počta, F.

1902. Anthozoaires et Alcyonaires. *in* Système Silurien du centre de la Bohême. by J. Barrande, Part 1, vol. 8, No. 2. The author, Prague, pp. i–viii + 1–347.

Potter, P. E., Maynard, J. B., and Pryor, W. A.

1980. Sedimentology of Shale; Study Guide and Reference Source. Springer-Verlag, New York, 310 pp.

Poulsen, C.

1941. The Silurian faunas of north Greenland, II: The fauna of the Offley Island Formation, Part 1, Coelenterata. Meddelelser om Grønland, vol. 72, No. 2, 27 pp.

Powell, J. H., and Scrutton, C. T.

1978. Variation in the Silurian tabulate coral *Paleofavosites asper*, and the status of *Mesofavosites*. Palaeontology, vol. 21, pp. 307–319.

Pryor, W. A., and Ross, C. A.

1962. Geology of the Illinois parts of the Cairo, La Center, and Thebes quadrangles. Illinois State Geological Survey, Circular 332, 39 pp.

Reeds, C. A.

1911. The Hunton Formation of Oklahoma. American Journal of Science, Series 4, vol. 32, pp. 256–268.

Raaaamusoks, A.

1960. Stratigraphy and paleogeography of the Ordovician in Estonia. *in* Proceedings of Section 7, Ordovician and Silurian stratigraphy and correlations. A.Martinsson and L.Störmer, *eds.*, International Geological Congress, Report of the Twenty-First Session, Norden, Part 7, pp. 58–69.

Rose, J. N.

1967. The fossils and rocks of eastern Iowa. Iowa Geological Survey, Educational Series, Publication 1, 147 pp.

Ross, C. A.

1962. Early Llandoverian (Silurian) graptolites from the Edgewood Formation, northeastern Illinois. Journal of Paleontology, vol. 36, pp. 1383–1386.

1964. Early Silurian graptolites from the Edgewood Formation of Iowa. Journal of Paleontology, vol. 38, pp. 1107, 1108.

Rowley, R. R.

1908. The geology of Pike County. Missouri Bureau of Geology and Mines, Series 2, vol. 8, 122 pp.

Rubey, W. W.

1952. Geology and mineral resources of the Hardin and Brussels quadrangles. United States Geological Survey, Professional Paper 218, 179 pp.

Sardeson, F. W.

1896. Ueber die Beziehungen der fossilen Tabulaten zu den Alcyonarien. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Bände 10, pp. 249–362.

Satterfield, I. R.

1971. Conodonts and stratigraphy of the Girardeau Limestone (Ordovician) of southeast Missouri and southwest Illinois. Journal of Paleontology, vol. 45, pp. 265–273.

Savage, T. E.

1910. The faunal succession and the correlation of the pre-Devonian formations of southern Illinois. Illinois State Geological Survey, Bulletin No. 16, Year-Book for 1909, pp. 302–341.

1912. The Channahon and Essex limestones in Illinois. Illinois Academy of Science, Transactions, vol. 4, pp. 97–103.

1913. Stratigraphy and paleontology of the Alexandrian Series in Illinois and Missouri; Part I. Illinois State Geological Survey, Extract from Bulletin No. 23, 124 pp.

1914. The relations of the Alexandrian Series in Illinois and Missouri to the Silurian section of Iowa. American Journal of Science, Series 4, vol. 38, pp. 28–37.

1917. Stratigraphy and paleontology of the Alexandrian Series in Illinois and Missouri; Part I. Illinois State Geological Survey, Bulletin No. 23, Biennial Report for 1911 and 1912, pp. 67–160.

1926. Silurian rocks of Illinois. Geological Society of America Bulletin, vol. 37, pp. 513–534.

Schouppé, A. von, and Oekentorp, K.

1974. Morphogenese und Bau der Tabulata, unter besonderer berücksichtigung der Favositida. Palaeontographica, Abteilung A, vol. 145, No. 4–6, pp. 79–194.

Scotese, C. R., and McKerrow, W. S.

1990. Revised world maps and introduction. *in* Palaeozoic Palaeogeography and Biogeography. W.S.McKerrow and C.R.Scotese, *eds.*, Geological Society of London, Memoir 12, pp. 1–21.

Scrutton, C. T.

1975. Corals and stromatoporoids from the Ordovician and Silurian of Kronprins Christian Land, northeast Greenland. Meddelelser om Grønland, vol. 171, No. 4, 43 pp.

1983. Astogeny in the Devonian rugose coral *Phillipsastrea nevadensis* from northern Canada. *in* Dorothy Hill jubilee memoir. P.A.Jell and J.Roberts, *eds.*, Association of Australasian Palaeontologists, Memoir 1, pp. 237–259.

1985. Anthozoa, Tabulata. *in* Atlas of Invertebrate Macrofossils. J.W.Murray, ed., Longman Group, London, pp. 31–36.

1987. A review of favositid affinities. Palaeontology, vol. 30, pp. 485–492.

1989. Intracolonial and intraspecific variation in tabulate corals. *in* Fossil Cnidaria 5; Proceedings of the Fifth International Symposium on Fossil Cnidaria Including Archaeocyatha and Spongiomorphs held in Brisbane, Queensland, Australia, 25–29 July 1988. P.A.Jell and J.W.Pickett, eds., Association of Australasian Palaeontologists, Memoir 8, pp. 33–43.

1990. Ontogeny and astogeny in *Aulopora* and its significance, illustrated by a new non-encrusting species from the Devonian of southwest England. Lethaia, vol. 23, pp. 61–75.

1993. Growth-form variation and control in two British Silurian species of *Propora*. *in* Proceedings of the VI. International Symposium on Fossil Cnidaria and Porifera held in Münster, Germany, 9–14 September 1991. P.Oekentorp-Küster, *ed.*, Courier Forschungs-Institut Senckenberg, vol. 164, pp. 273–281.

Scrutton, C. T., and McCurry, J. A.

1987. The derivation, biostratigraphy and palaeobiogeographic significance of corals from Silurian deep-sea turbidite facies in the south-west Southern Uplands. Scottish Journal of Geology, vol. 23, pp. 49–64.

Scrutton, C. T., and Powell, J. H.

1980. Periodic development of dimetrism in some favositid corals. Acta Palaeontologica Polonica, vol. 25, pp. 477–491.

Sepkoski, J. J., Jr.

1986. Phanerozoic overview of mass extinction. *in* Patterns and Processes in the History of Life. D.M.Raup and D.Jablonski, *eds.*, Springer-Verlag, Berlin, pp. 277–295.

Sheehan, P. M.

1973. The relation of Late Ordovician glaciation to the Ordovician–Silurian changeover in North American brachiopod faunas. Lethaia, vol. 6, pp. 147–154.

1988. Late Ordovician events and the terminal Ordovician extinction. *in* Contributions to Paleozoic paleontology and stratigraphy in honor of Rousseau H. Flower. D.L. Wolberg, compiler, New Mexico Bureau of Mines and Mineral Resources, Memoir 44, pp. 405–415.

Shimizu, S., Ozaki, K., and Obata, T.

1934. Gotlandian deposits of northwest Korea. Shanghai Science Institute, Journal, sec. 2, vol. 1, pp. 59–88.

Shrock, R. R., and Twenhofel, W. H.

1953. Principles of Invertebrate Paleontology. McGraw-Hill, New York, 816 pp.

Simpson, G. G., Roe, A., and Lewontin, R. C.

1960. Quantitative Zoology. Revised Edition. Harcourt, Brace, and Company, New York, 440 pp.

Sinclair, G. W.

1955. Some Ordovician halysitoid corals. Royal Society of Canada, Transactions, vol. 49, Series 3, sec. 4, pp. 95–103.

Skidmore, W. B., and Lespérance, P. J.

1981. Percé area. *in* Field Meeting, Anticosti–Gaspé, Québec, 1981; vol. 1, Guidebook. P.J.Lespérance, *ed.*, Département de géologie, Université de Montréal, pp. 31–40.

Sloan, R. E.

1987. Tectonics, biostratigraphy and lithostratigraphy of the Middle and Late Ordovician of the Upper Mississippi Valley. *in* Middle and Late Ordovician lithostratigraphy and biostratigraphy of the Upper Mississippi Valley. R.E.Sloan, *ed.*, Minnesota Geological Survey, Report of Investigations 35, pp. 7–20.

Sokolov, B. S.

1947. Novye syringoporidy Taymyra. Moskovskogo Obshchestva Ispytatelei Prirody, Byulletin (Geologiia), vol. 22, Part 6, pp. 19–28.

1949. Tabulata i Heliolitida. *in* Atlas rukovodyashchikh form iskopaemykh faun SSSR, II: Siluryskaya sistema. Gosgeoltekhizdat, Moscow, pp. 75–98.

1950a. Sistematika i istoriya razvitiya paleozoyskikh korallov Anthozoa Tabulata. Voprosy Paleontologii, vol. 1, pp. 134–210.

1950b. Siluriiskie korally zapada Sibirskoi platformy. Voprosy Paleontologii, vol. 1, pp. 211–242.

1951a. Tabulyaty paleozoya evropeyskoy chasti SSSR, chast 1: Ordovik zapadnogo Urala i Pribaltiki. Vsesoiuznyi Neftyanoy Nauchno-Issledovatelskii Geologo-Razvedochny Institut (VNIGRI), Trudy, New Series, vol. 48, 132 pp.

1951b. Tabulyaty paleozoya evropeyskoy chasti SSSR, chast 2: Silur Pribaltiki (Favozitidy llandoverskogo yarusa). Vsesoiuznyi Neftyanoy Nauchno-Issledovatelskii Geologo-Razvedochny Institut (VNIGRI), Trudy, New Series, vol. 52, 124 pp.

1955. Tabulyaty paleozoya evropeyskoy chasti SSSR, Vvedenie: Obshchie voprosy sistematiki i istorii razvitiya tabulyat. Vsesoiuznyi Neftyanoy Nauchno-Issledovatelskii Geologo-Razvedochny Institut (VNIGRI), Trudy, New Series, vol. 85, 527 pp.

1962. Biostratigraficheskiy i biogeograficheskiy obzor tabulyatomorfnykh korallov paleozoya SSSR. Akademiya Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii i Geofiziki, 1962, No. 10, pp. 53–67.

Sokolov, B. S., and Tesakov, Yu. I.

1963. Tabulyaty Paleozoya Sibiri; Tabulyaty Ordovika i Silura Vostochnoy Chasti Sibiri. Sibirskoe Otdelenie Institut Geologii i Geofiziki, Izdatelstvo Akademii Nauk SSSR, 148 pp.

Stanton, L. J., Sheehan, P. M., and Lespérance, P. J.

1990. Brachiopod faunal replacement across the Ordovician–Silurian extinction event in Missouri. *in* Paleocommunity temporal dynamics: the long-term development of multispecies assemblies. W.Miller, III, *ed.*, Paleontological Society, Special Publication No. 5, pp. 71–84.

Stasinska, A.

1967. Tabulata from Norway, Sweden and from the erratic boulders of Poland. Palaeontologia Polonica, No. 18, pp. 1–112.

Stearn, C. W.

1956. Stratigraphy and palaeontology of the Interlake Group and Stonewall Formation of southern Manitoba. Geological Survey of Canada, Memoir 281, 162 pp.

1989. Intraspecific variability and species concepts in Palaeozoic stromatoporoids. *in* Fossil Cnidaria 5. Proceedings of the Fifth International Symposium on Fossil Cnidaria Including Archaeocyatha and Spongiomorphs held in Brisbane, Queensland, Australia, 25–29 July 1988. P.A.Jell and J.W.Pickett, *eds.*, Association of Australasian Palaeontologists, Memoir 8, pp. 45–50.

Stechow, E.

1922. Zur Systematik der Hydrozoen, Stromatoporen, Siphonophoren, Anthozoen und Ctenophoren. Archiv für Naturgeschichte, vol. 88A (3), pp. 141–155.

Stel, J. H.

1975. Erratische Favositidae der nördlichen Niederlande. Der Geschiebe-Sammler, Hamburg, Sonderheft 2, 203 pp.

Stel, J. H., and Oekentorp, K.

1976. On the solenid growth habit of Paleofavosites. Geologie en Mijnbouw, vol. 55(3–4), pp. 163–174.

1980. *Desmidopora* and *Nodulipora*: misfits in the coral world. Acta Palaeontologica Polonica, vol. 25, pp. 403–417.

Stimpson, W.

1858. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem . . . Pars VII. Academy of Natural Sciences of Philadelphia, Proceedings, pp. 225–252.

Stumm, E. C.

1965. Silurian and Devonian corals of the Falls of the Ohio. Geological Society of America, Memoir 93 (1964), 184 pp.

Sutton, I. D.

1966. The value of corallite size in the specific determination of the tabulate corals *Favosites* and *Palaeofavosites*. Mercian Geologist, vol. 1, pp. 255–263.

Swallow, G. C.

1855. Geology of Missouri. *in* The First and Second Annual Reports of the Geological Survey of Missouri, Part 1. by G.C.Swallow, Missouri Geological Survey, pp. 59–170.

Sweet, W. C.

1979. Late Ordovician conodonts and biostratigraphy of the Western Midcontinent Province. *in* Conodont biostratigraphy of the Great Basin and Rocky Mountains. C.A. Sandberg and D.L.Clark, *eds.*, Brigham Young University, Geology Studies, vol. 26, Part 3, pp. 45–85.

1984. Graphic correlation of upper Middle and Upper Ordovician rocks, North American Midcontinent Province, U.S.A. *in* Aspects of the Ordovician System. D.L.Bruton, *ed.*, Palaeontological Contributions from the University of Oslo, No. 295, pp. 23–35.

Taylor, P. D.

1990. Encrusters. *in* Palaeobiology: A Synthesis. D.E.G.Briggs and P.R. Crowther, *eds.*, Blackwell Scientific, Cambridge, MA, pp. 346–351.

Tesakov, Yu. I.

1973. Izmenchivost diametra korallitov i por u *Favosites gothlandicus* i ee svyazi s usloviyami obitaniya. *in* Sreda i zhizn'v Geologicheskom Proshlom (Pozdniy dokembriy i paleozoy Sibiri). O.A.Betekhtina, *et al.*, *eds.*,Trudy Instituta Geologii i Geofiziki, pp. 84–92.

Thompson, T. L., and Satterfield, I. R.

1975. Stratigraphy and conodont biostratigraphy of strata contiguous to the Ordovician–Silurian boundary in eastern Missouri. Missouri Geological Survey, Report of Investigations No. 57, Studies in Stratigraphy, Part 2, pp. 61–108.

Twenhofel, W. H.

1914. The Anticosti Island faunas. Geological Survey of Canada, Museum Bulletin No. 3, Geological Series No. 19, 39 pp.

1916. Part 2, The Silurian and high Ordovician strata of Esthonia, Russia, and their faunas. Harvard College, Museum of Comparative Zoology, Bulletin 56, Geological Series 10, No. 4, pp. 289–340.

1928. Geology of Anticosti Island. Geological Survey of Canada, Memoir 154, 481 pp.

Veron, J. E. N., and Pichon, M.

1976. Scleractinia of eastern Australia, Part I: Families Thamnasteriidae, Astrocoeniidae, Pocilloporidae. Australian Institute of Marine Science, Monograph Series, vol. 1, 86 pp.

Verrill, A. E.

1865. Classification of polyps (Extract condensed from a synopsis of the polypi of the North Pacific Exploring Expedition, under Captains Ringgold and Rodgers, U.S.N.). Essex Institute, Proceedings, vol. 4, pp. 145–149.

Volkova, K. N., Latypov, Yu. Ya., and Khayznikova, K. B.

1978. Ordovik i silur Yuzhnogo Verkhoyan'ya (biostratigrafiya i paleontologiya). Trudy Instituta Geologii i Geofiziki (Novosibirsk), vol. 381, 222 pp.

Webby, B. D.

1975. Patterns of increase in coenosteoid halysitid corals. Alcheringa, vol. 1, pp. 31–36.

1977. Upper Ordovician tabulate corals from central-western New South Wales. Linnean Society of New South Wales, Proceedings, vol. 101, Part 3, pp. 167–183.

Webby, B. D., and Semeniuk, V.

1969. Ordovician halysitid corals from New South Wales. Lethaia, vol. 2, pp. 345–360.

1971. The Ordovician coral genus *Tetradium* Dana from New South Wales. Linnean Society of New South Wales, Proceedings, vol. 95, Part 3, pp. 246–258.

Webby, B. D., VandenBerg, A. H. M., Cooper, R. A., Banks, M. R., Burrett, C. F., Henderson, R. A., Clarkson, P. D., Hughes, C. P., Laurie, J., Stait, B., Thomson, M. R. A., and Webers, G. F.

1981. The Ordovician System in Australia, New Zealand and Antarctica; correlation chart and explanatory notes. International Union of Geological Sciences, Publication No. 6, 64 pp.

Wedekind, R.

1937. Einführung in die Grundlagen der historischen Geologie, II. Band. Mikrobiostratigraphie, Die Korallen-und Foraminiferenzeit. Ferdinand Enke, Stuttgart, 136 pp.

Weller, J. M.

1940. Explanation and stratigraphic summary. *in* Preliminary geologic map of parts of the Alto Pass, Jonesboro, and Thebes quadrangles, Union, Alexander, and Jackson counties. by J.M.Weller and G.E.Ekblaw. Illinois State Geological Survey, Report of Investigations, No. 70, pp. 1–26.

Whiteaves, J. F.

1884. On some new, imperfectly characterized or previously unrecorded species of fossils from the Guelph Formation of Ontario. Geological Survey of Canada, Palaeozoic Fossils, vol. 3, Part 1, pp. 1–43.

Whitlow, J. W., and Brown, C. E.

1963. The Ordovician–Silurian contact in Dubuque County, Iowa. United States Geological Survey, Professional Paper 475-C, pp. 11–13.

Willis, B. L., and Ayre, D. J.

1985. Asexual reproduction and genetic determination of growth form in the coral *Pavona cactus*: biochemical genetic and immunogenic evidence. Oecologia, vol. 65, pp. 516–525.

Willman, H. B.

1962. Description of stops, second day. *in* Silurian Rocks of the Southern Lake Michigan Area, Michigan Basin Geological Society, Annual Field Conference, 1962. Michigan Geological Survey, pp. 81–96

1973. Rock stratigraphy of the Silurian System in northeastern and northwestern Illinois. Illinois State Geological Survey, Circular 479, 55 pp.

Winchell, H. H., and Schuchert, C.

1895. Chapter 3: Sponges, graptolites, and corals from the Lower Silurian of Minnesota. *in* The Geology of Minnesota; vol. 3, Part 1, Paleontology. Minnesota Geological and Natural History Survey, pp. 55–95.

Winder, G. C., and Sanford, B. V.

1972. Stratigraphy and paleontology of the Paleozoic rocks of southern Ontario. 24th International Geological Congress, Guidebook to Excursion A45-C45, 74 pp.

Witzke, B. J.

1992. Silurian stratigraphy and carbonate mound facies of eastern Iowa; field trip guidebook to Silurian exposures in Jones and Linn counties. Iowa Department of Natural Resources, Guidebook Series No. 11, 111 pp.

Witzke, B. J., and Kolata, D. R.

1988. Changing structural and depositional patterns, Ordovician Champlainian and Cincinnatian series of Iowa–Illinois. *in* New perspectives on the Paleozoic history of the Upper Mississippi Valley: an examination of the Plum River Fault Zone. G.A.Ludvigson and B.J.Bunker, *eds.*, Iowa Department of Natural Resources, Guidebook No. 8, pp. 55–77.

Worsley, D., Aarhus, N., Bassett, M. G., Howe, M. P. A., Mørk, A., and Olaussen, S.

1983. The Silurian succession of the Oslo region. Norges geologiske undersøkelse, No. 384, 57 pp.

Worthen, A. H.

1866. Devonian and Silurian systems, in Vol. 1, Geology. Illinois State Geological Survey, pp. 119–152.

Yabe, H.

1915. Einige Bemerkungen ueber die *Halysites*-Arten. Tôhoku Imperial University, Science Reports, Series 2 (Geology), vol. 4, pp. 25–38.

Young, G. A.

1988. Paleoecology, Biostratigraphy, and Systematics of Silurian Tabulate Corals from the Chaleur Bay Region, Eastern Canada. unpublished PhD thesis, University of New Brunswick, Fredericton, 520 pp.

Young, G. A., and Elias, R. J.

1993. Biometry and intraspecific variation in favositid and heliolitid corals. *in* Proceedings of the VI. International Symposium on Fossil Cnidaria and Porifera held in Münster, Germany 9.–14. September 1991. P.Oekentorp-Küster, *ed.*, Courier Forschungs-Institut Senckenberg, vol. 164, pp. 283–291.

Young, G. A., Lee, D.-J., and Noble, J. P. A.

1991. Halysitid and auloporid tabulate corals from the Gascons and West Point formations (Silurian), Gaspé, Québec, Canada. Journal of Paleontology, vol. 65, pp. 715–726.

Young, G. A., and Noble, J. P. A.

1989. Variation and growth of a syringoporid symbiont species in stromatoporoids from the Silurian of eastern Canada. *in* Fossil Cnidaria 5. Proceedings of the Fifth International Symposium on Fossil Cnidaria Including Archaeocyatha and Spongiomorphs. P.A. Jell and J.W.Pickett, eds., Association of Australasian Palaeontologists, Memoir 8, pp. 91–98.

1990a. Silurian Heliolitidae (Anthozoa, Tabulata) from the Chaleurs Bay region, Canada. Journal of Paleontology, vol. 64, pp. 44–60.

1990b. Silurian Proporidae and Plasmoporidae (Anthozoa, Tabulata) from the Chaleurs Bay region, Canada. Journal of Paleontology, vol. 64, pp. 184–199.

Young, G. A., and Scrutton, C. T.

1991. Growth form in Silurian heliolitid corals: the influence of genetics and environment. Paleobiology, vol. 17, pp. 369–387.

Yü Chang-ming

1960. Late Ordovician corals of China [Chinese with Russian summary]. Acta Palaeontologica Sinica, vol. 8, No. 2, pp. 65–132.

PLATES

Exterior views are of specimens coated with ammonium chloride. Transverse and longitudinal sections are photomicrographs of thin sections. For serial transverse sections, orientation of the specimen remains the same from one figure to the next. Longitudinal sections are oriented with the direction of growth toward the top of the plate.

EXPLANATION OF PLATE 1

Figure Page

1–11. ***Propora thebesensis*** (Foerste, 1909) 45

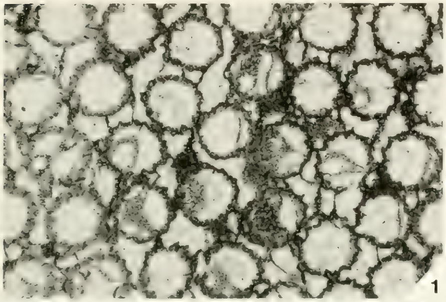
[1–11, *Brevilamnulella* beds, Keel Formation, Section-interval 23-2 (Lawrence Quarry) (1, 2, 4–9, site 23iii; 3, site 23i; 10, 11, site 23ii).]

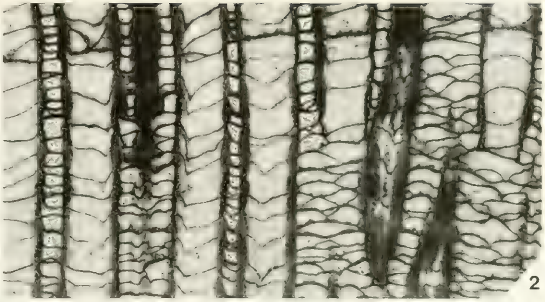
1, 2. USNM 485706a: 1, transverse section, ×8; 2, longitudinal section, ×8.

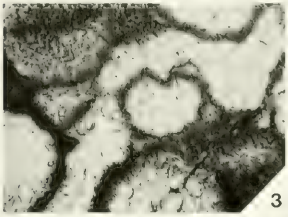
3. USNM 485700: transverse section showing new tabularium, ×20.

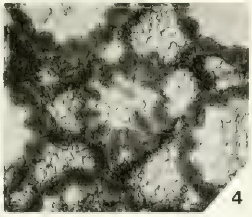
4–9. USNM 458777: 4, transverse section showing new tabularium, ×20; 5, transverse section, ×8; 6, 7, transverse sections, ×40; 8, longitudinal section showing growth around crinoid grain, ×8; 9, longitudinal oblique section of a corallite, showing trabeculae, ×40.

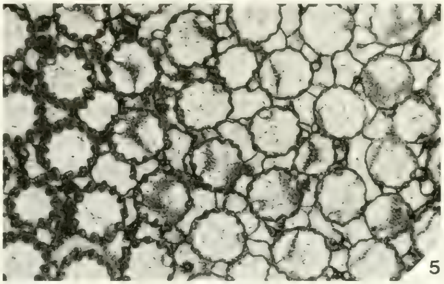
10, 11. USNM 485703: 10, transverse section, ×8; 11, longitudinal section, ×8.

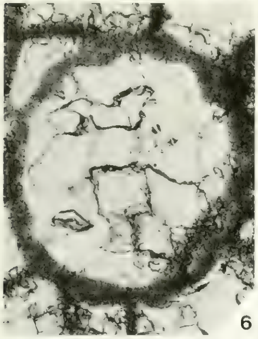

1

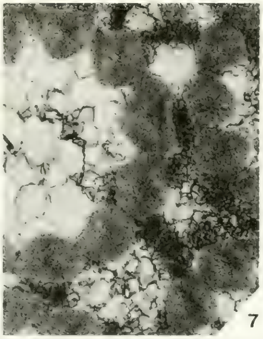

2

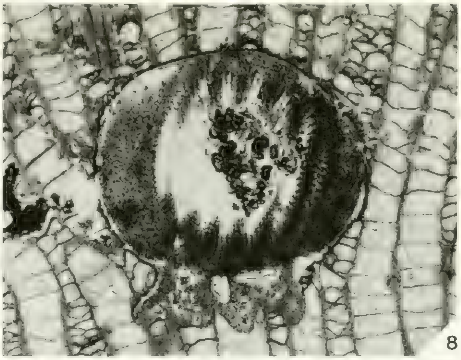

3

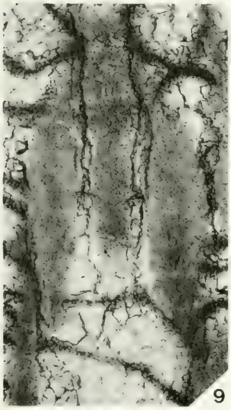

4

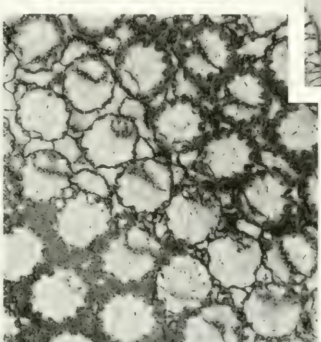

5

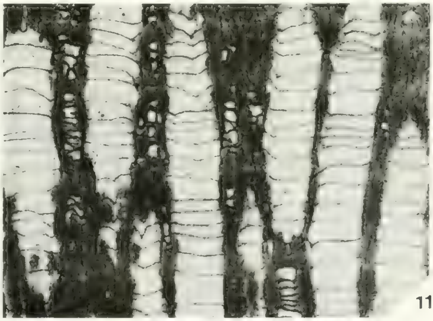

6

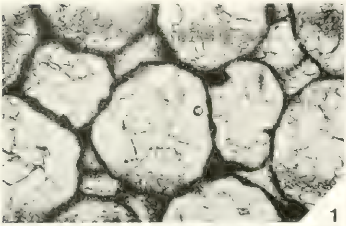

7

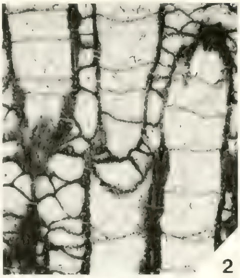

8

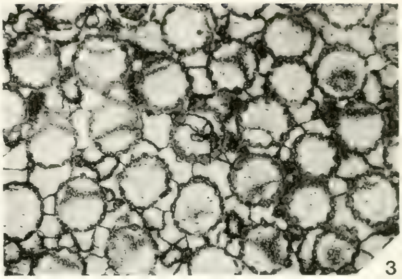

9

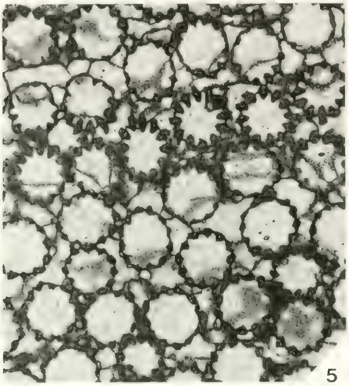

10

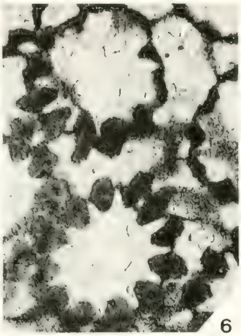

11

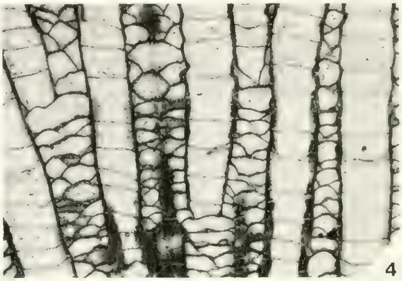

1

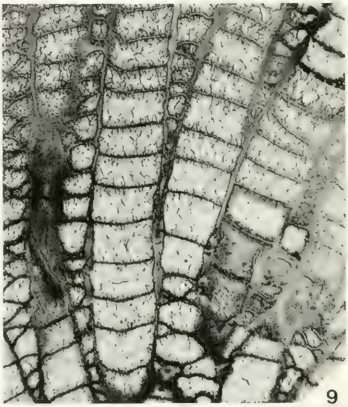

2

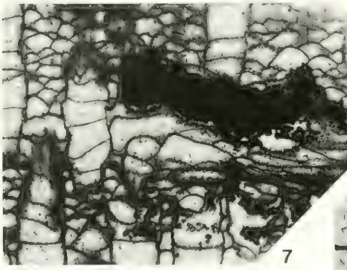

3

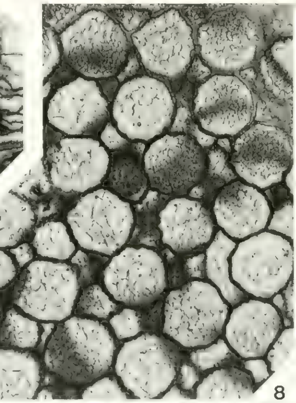

5

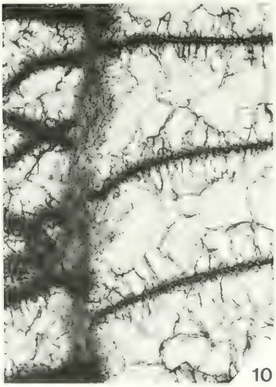

6

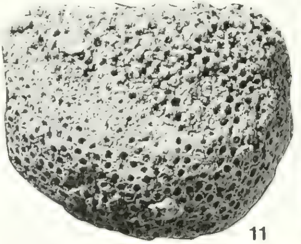

4

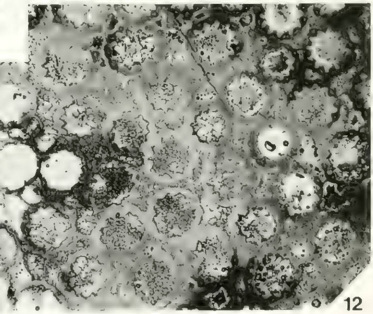

9


7


8


10


11


12

EXPLANATION OF PLATE 2

Figure		Page
1–12.	***Propora thebesensis*** (Foerste, 1909)	45

[1–4, *Brevilamnulella* beds, Keel Formation, Section-interval 23-2 (Lawrence Quarry) (site 23iii); 5–7, oölite of Keel Formation, Section-interval 23-2a (Lawrence Quarry) (site 23i); 8–10, Leemon Formation, Section-interval 31-1 (Thebes North); 11, 12, Leemon Formation (undivided), Section 31 (Thebes North).]

1. USNM 485706b: transverse section, ×15.
2–4. USNM 459075: 2, longitudinal section showing rejuvenescence, ×12; 3, transverse section, ×8; 4, longitudinal section, ×8.
5, 6. USNM 485709: 5, transverse section, ×8; 6, transverse section (detail from upper left of center in 5, turned 50° clockwise), ×20.
7. USNM 485708: longitudinal section showing sediment inclusion and regeneration, ×12.
8–10. USNM 485711: 8, transverse section, ×8; 9, longitudinal section, ×8; 10, longitudinal section showing tabularium wall, ×40.
11, 12. UI X-908: 11, exterior lateral view of corallum, ×1.5; 12, transverse section, ×8.

EXPLANATION OF PLATE 3

Figure Page

1–11. ***Propora thebesensis*** (Foerste, 1909) 45

[1–3, Leemon Formation (undivided), Section 31 (Thebes North); 4, Leemon Formation, Section-interval 31-1 (Thebes North); 5, Bryant Knob Formation (undivided), 5 km south of Clarksville, Missouri; 6, 7, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 18-4 (Kissenger); 8–11, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 16-2 (Clinton Spring).]

1, 2. USNM 84863b (lectotype): 1, transverse section, ×8; 2, exterior lateral view of corallum, ×1.5.

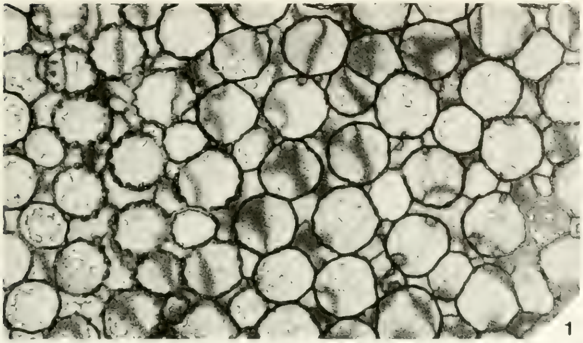
3. USNM 84863a (paralectotype): exterior basal view of corallum, ×2.

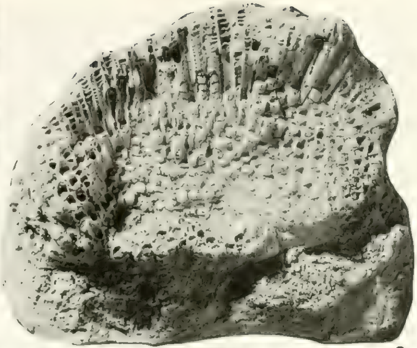
4. USNM 485715: longitudinal section through entire corallum (note abraded base), ×2.

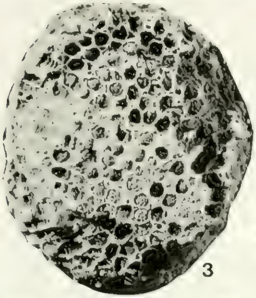
5. UI C-1466b: transverse section, ×8.

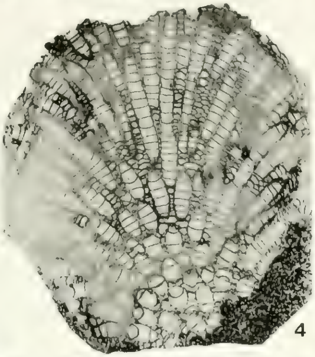
6, 7. USNM 459084: 6, transverse section, ×8; 7, longitudinal section, ×8.

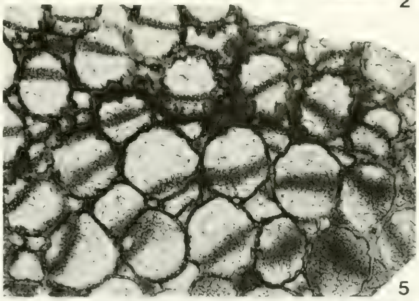
8–11. USNM 459076: 8, longitudinal section through entire corallum (note abrasion at base), ×2; 9, transverse section, ×8; 10, longitudinal section (detail from lower left of center in 8, turned 20° counterclockwise), ×8; 11, longitudinal section through base of a tabularium (detail from center of 10), ×15.

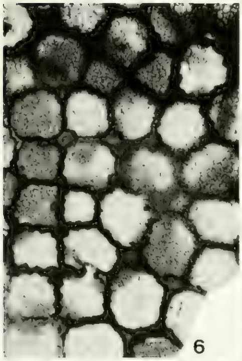

1

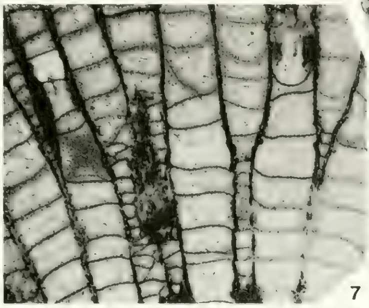

2

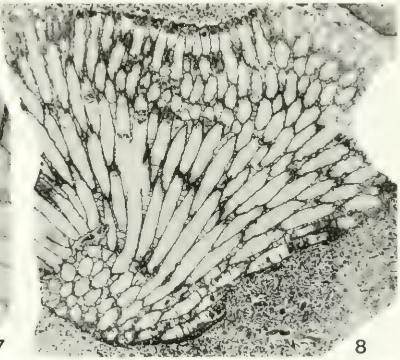

3

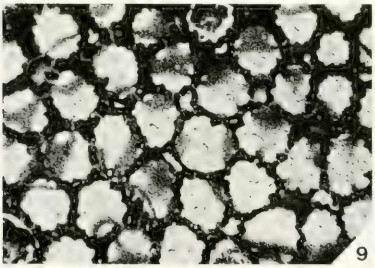

4

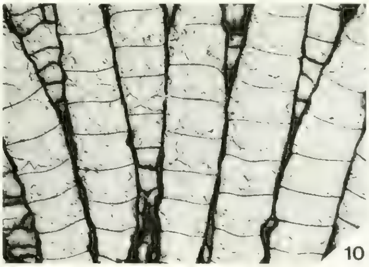

5

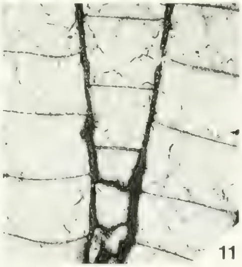

6

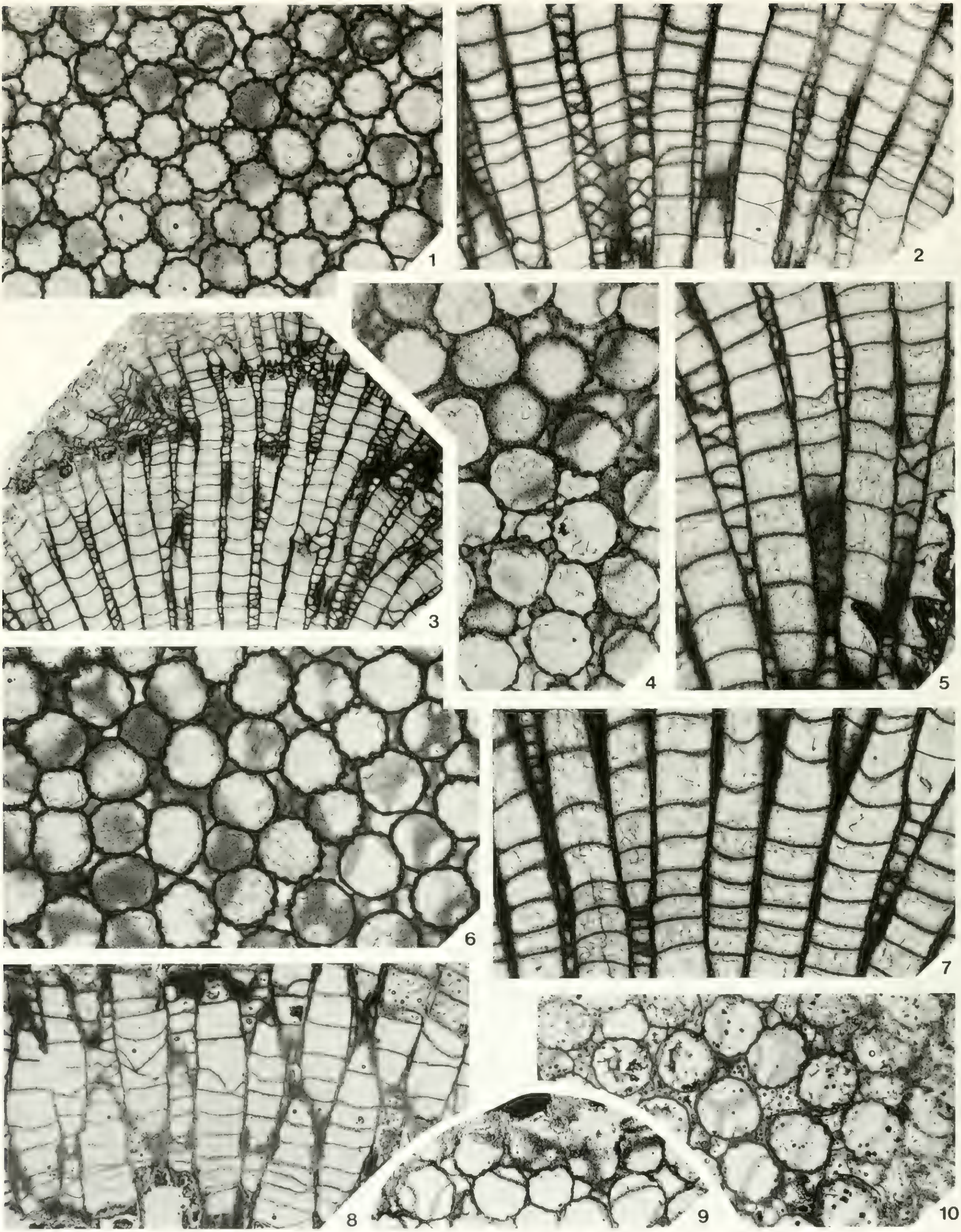

7


8


9


10


11


1
2
3
4
5
6
7
8
9
10

EXPLANATION OF PLATE 4

Figure — Page

1–10. ***Propora thebesensis*** (Foerste, 1909) 45

[1, 2, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 15-1 (Calumet); 3–7, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 14-1 (Higginbotham Farm); 8, coral-rich bedding surface of Mosalem Formation, Section-interval 32-1z (Thomson East); 9, 10, upper Mosalem Formation, Section-interval 32-1c (Thomson East).]

1, 2. USNM 485729: 1, transverse section, ×8; 2, longitudinal section, ×8.
3. USNM 485754: longitudinal section showing partial mortality and regeneration, ×5.
4, 5. USNM 485755: 4, transverse section, ×8; 5, longitudinal section, ×8.
6, 7. USNM 485753: 6, transverse section, ×8; 7, longitudinal section, ×8.
8. USNM 485758: longitudinal section, ×8.
9. USNM 485760: transverse section, ×8.
10. USNM 485762: transverse section, ×8.

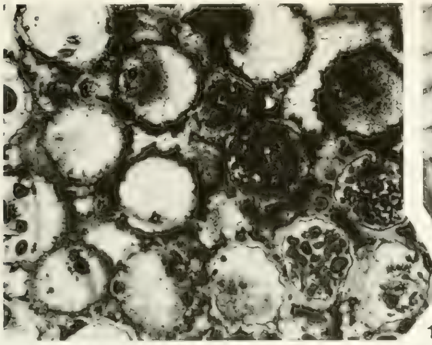
EXPLANATION OF PLATE 5

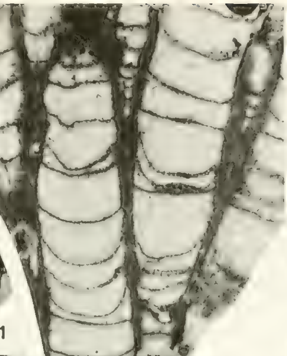
Figure Page

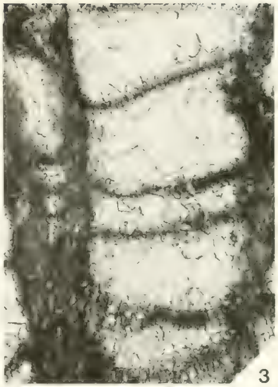
1–10. ***Propora savagei,*** new species 56

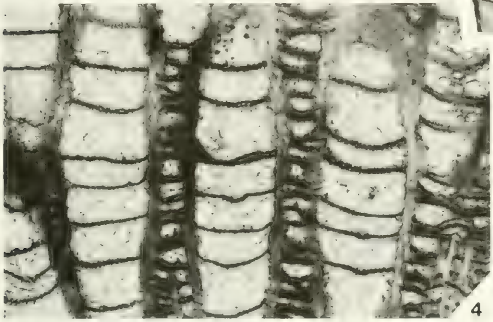
[1–3, oölite of Keel Formation, Section-interval 23-3 (Lawrence Quarry) (site 23ii); 4, Leemon Formation, Section-interval 31-1 (Thebes North); 5, 6, Leemon Formation (undivided), Section 31 (Thebes North); 7–10, Leemon Formation, Section-interval 20-6 (Short Farm).]

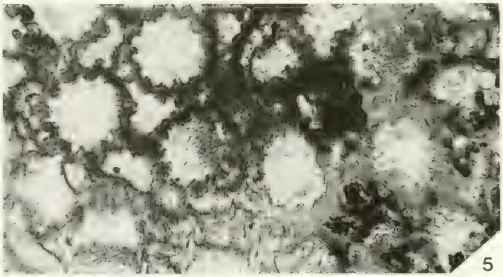
- 1–3. USNM 485764 (paratype): 1, transverse section, ×8; 2, longitudinal section, ×8; 3, longitudinal section through a tabularium, ×20.
- 4. USNM 485769: longitudinal section, ×8.
- 5, 6. UI X-8722 (holotype): 5, transverse section, ×8; 6, longitudinal section showing sediment inclusion and rejuvenescence, ×8.
- 7–10. USNM 485766 (paratype): 7, transverse section, ×40; 8, longitudinal section showing regeneration in a composite corallum, ×8; 9, transverse section, ×8; 10, longitudinal section, ×8.

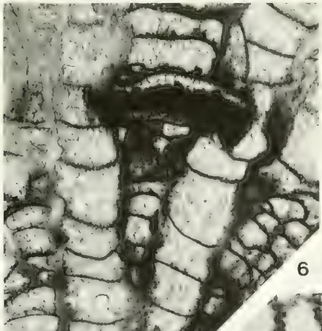

1

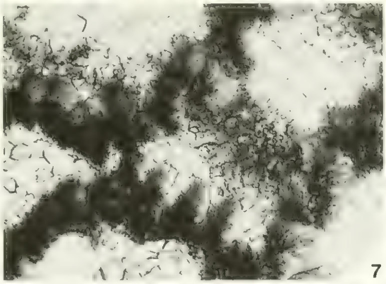

2

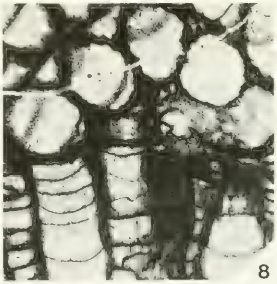

3

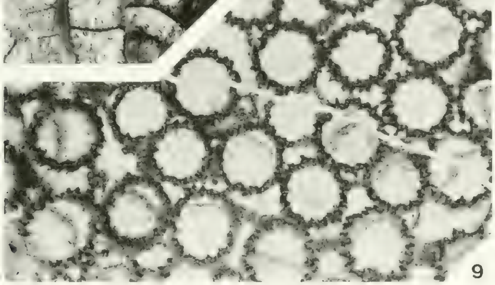

4

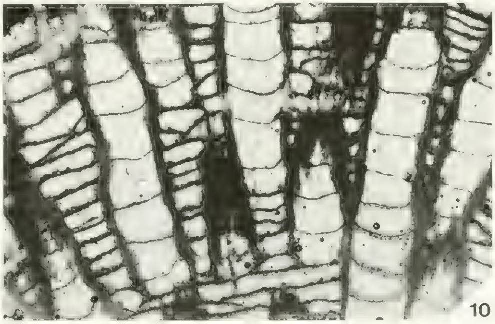

5

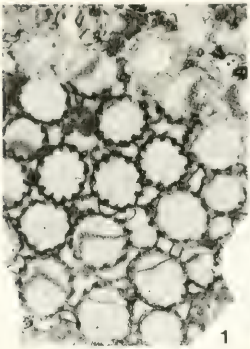

6

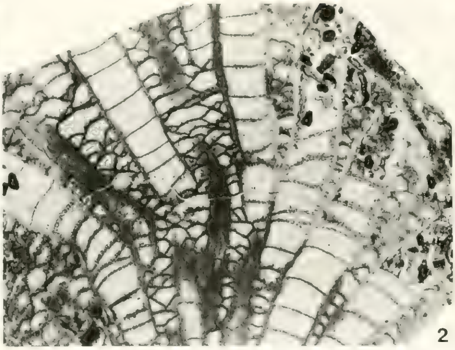

7

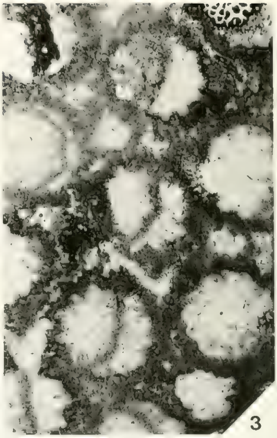

8

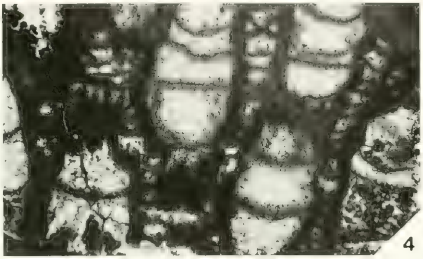

9

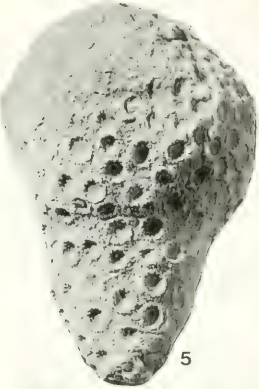

10

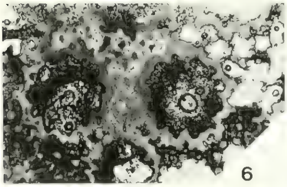

1

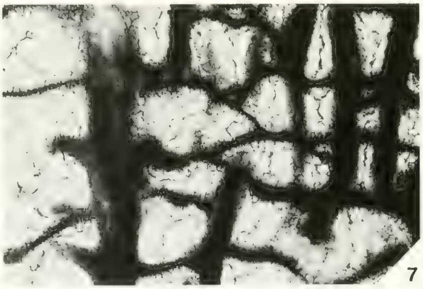

2

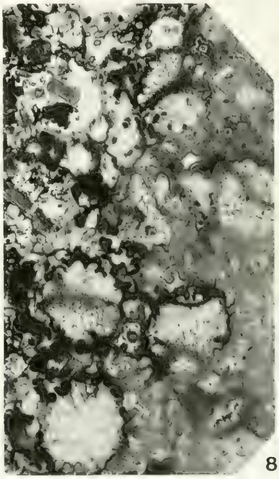

3

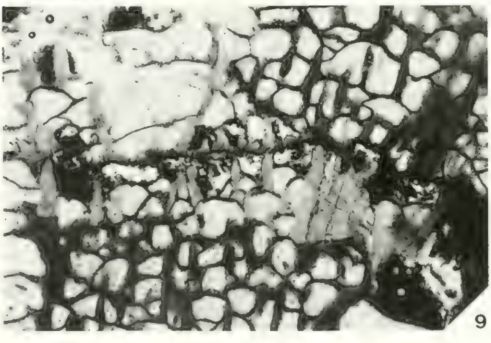

4

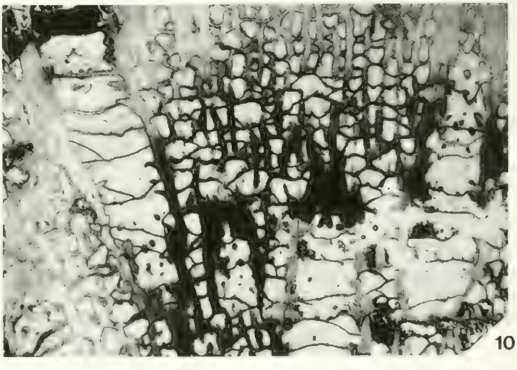

5


6


7


8


9

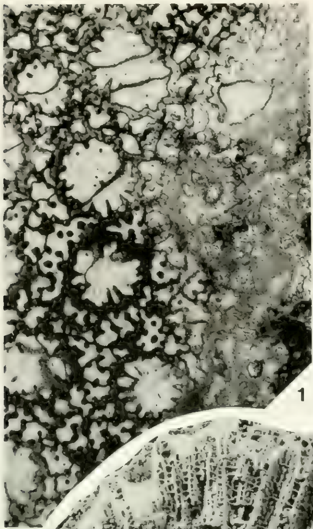

10

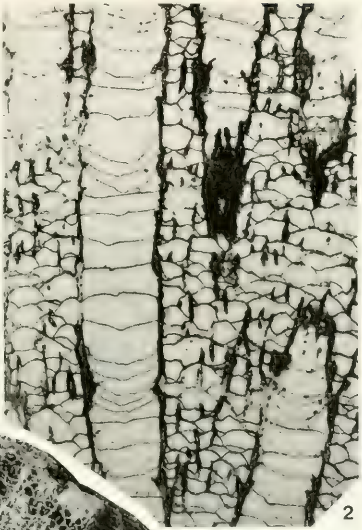
EXPLANATION OF PLATE 6

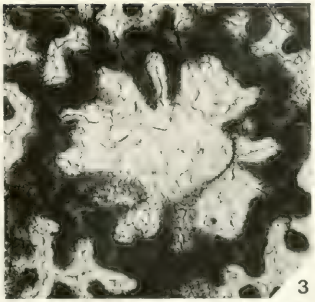
Figure		Page
1–4.	**Propora savagei,** new species	56
	[1, 2, Leemon Formation, Section-interval 20-1 (Short Farm); 3, 4, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 14-1 (Higginbotham Farm).]	
	1, 2. USNM 485765 (paratype): 1, transverse section, ×8; 2, longitudinal section, ×8.	
	3, 4. USNM 485775: 3, transverse section, ×8; 4, longitudinal oblique section, ×8.	
5–10.	**Propora speciosa** (Billings, 1865)	58
	[5, Ellis Bay Formation, White Cliff, Anticosti Island, Québec; 6–10, Leemon Formation, Section 31 (Thebes North).]	
	5. GSC 2240a (lectotype): exterior lateral view of corallum, ×1.5.	
	6. UI C-1438: transverse section, ×5.	
	7–10. UI C-889a: 7, longitudinal section showing trabecular rods in coenenchyme (detail from left of center in 10, turned 20° clockwise), ×20; 8, transverse section, ×5; 9, longitudinal section showing regeneration, ×8; 10, longitudinal section, ×5.	

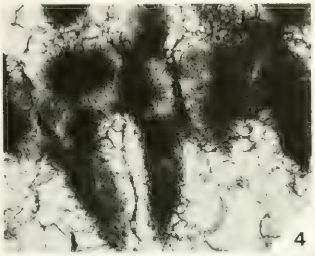
EXPLANATION OF PLATE 7

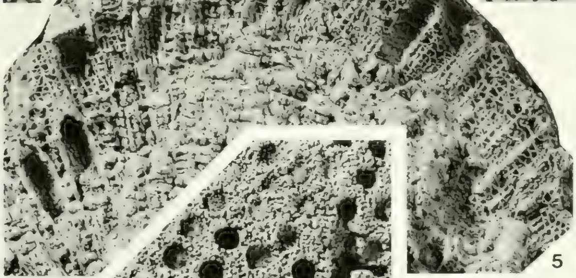
Figure		Page
1–8.	***Propora speciosa*** (Billings, 1865)	58
	[1–7, Leemon Formation, Gale Section; 8, upper Mosalem Formation, Section-interval 32-1c (Thomson East).]	
	1–6. UI X-850: 1, transverse section, ×5; 2, longitudinal section, ×5; 3, transverse section (detail from lower left of center in 1, turned 180°), ×15; 4, transverse section (detail from top center in 3) showing septal structure, ×40; 5, exterior view of broken longitudinal surface, ×2; 6, exterior view of transverse surface, ×2.	
	7. UI C-1440: transverse section, ×5.	
	8. USNM 485776: transverse section, ×5.	
9, 10.	***Propora*** species aff. ***P. affinis*** (Billings, 1865)	62
	[Elwood Formation, Section-interval 29-4 (Sears Pit).]	
	9, 10. USNM 485777: 9, transverse section, ×8; 10, longitudinal section, ×8.	

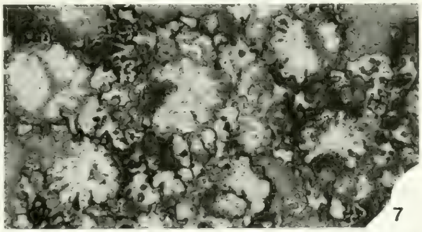

1

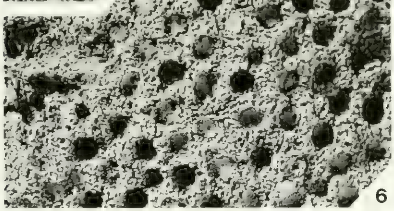

2

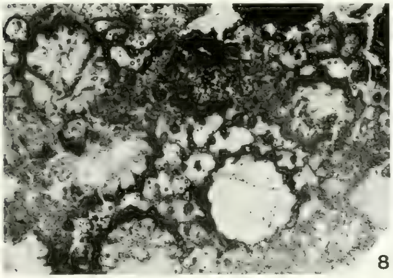

3

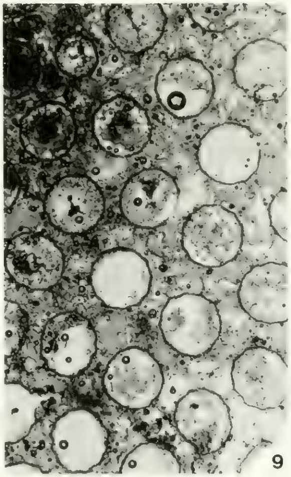

4

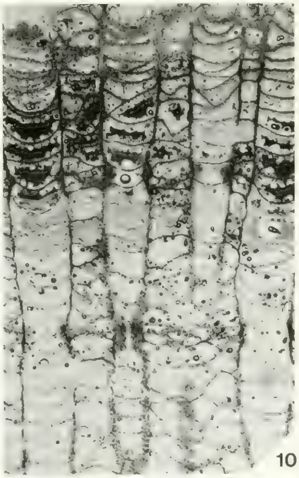

5

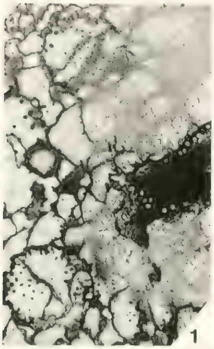

7

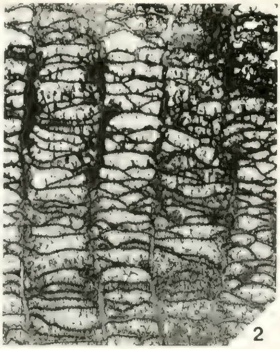

6

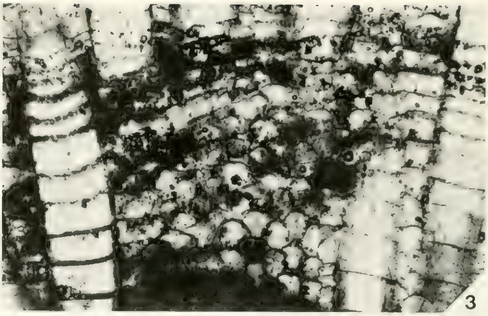

8

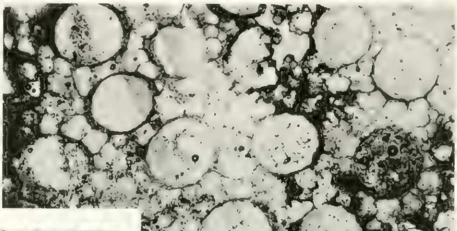

9

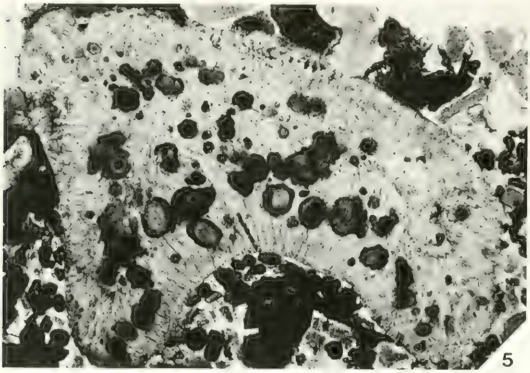

10

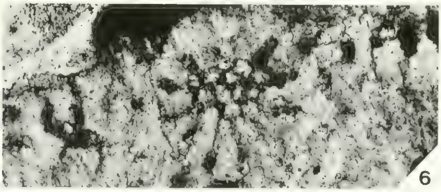

1

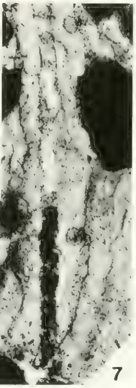

2

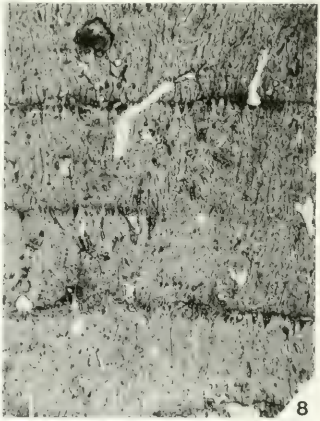

3

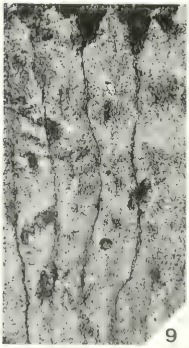

4

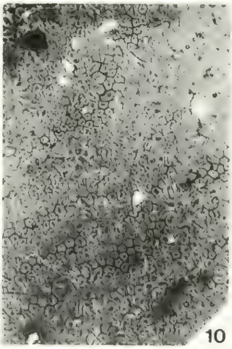

5

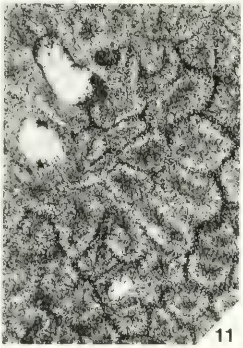

6

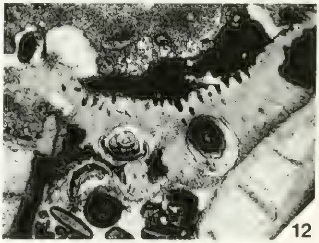

7


8


9


10


11


12

EXPLANATION OF PLATE 8

Figure		Page
1, 2.	**Propora** species A	63
	[1, 2, Sexton Creek Limestone, near Thebes, Illinois.]	
	1, 2. UI C-1403: 1, transverse section, ×5; 2, longitudinal section, ×5.	
3, 4.	**Plasmopora** species cf. ***P. logani*** Young and Noble, 1990b	64
	[3, 4, Cyrene Formation, near Edgewood, Missouri.]	
	3, 4. UI C-865b: 3, longitudinal section, ×8; 4, transverse section, ×8.	
5–7.	**Acidolites** species A	65
	[5–7, Leemon Formation, Section 31 (Thebes North).]	
	5–7. UI C-889b: 5, section through entire corallum (includes longitudinal and transverse sections of corallites), ×10; 6, transverse section showing a single tabularium (detail from top center of corallum in 5, turned 30° counterclockwise), ×40; 7, longitudinal section (detail from bottom center of corallum in 5), ×40.	
8–12.	**Protaraea** species A	66
	[8–12, *Brevilamnulella* beds, Keel Formation, Section-interval 23-2 (Lawrence Quarry) (8–11, site 23i; 12, site 23iv).]	
	8–11. USNM 485778: 8, longitudinal section (dark horizontal layers are sediment inclusions), ×8; 9, longitudinal section, ×40; 10, transverse section, ×8; 11, transverse section showing a single tabularium (detail from upper left of center in 10), ×40; note microborings in 8–11 (micrite-filled microborings are darker than corallum, cement-filled microborings are lighter).	
	12. USNM 485780c: longitudinal section showing corallum (center) encrusting corallites of *Halysites alexandricus* (lower left, lower right), ×12.	

EXPLANATION OF PLATE 9

Figure		Page
1–11.	***Halysites alexandricus,*** new species	67

[1–8, *Brevilamnulella* beds, Keel Formation, Section-interval 23-2 (Lawrence Quarry) (1–3, site 23i; 4–6, site 23ii; 7, site 23iv; 8, site 23iii); 9–11, Keel Formation (undivided), Section-interval 23a-1 (Lawrence Quarry).]

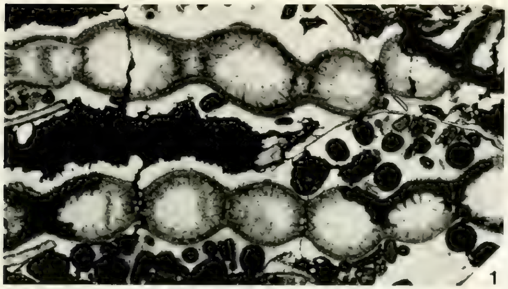
1–3. USNM 485782 (paratype): 1, transverse section, ×8; 2, transverse section, ×20; 3, transverse section showing wall structure, ×40.

4–6. USNM 458778 (paratype): 4, transverse section, ×8; 5, longitudinal section, ×8; 6, longitudinal section showing structure of walls and tubule (detail from lower right of center in 5, turned 10° counterclockwise), ×40.

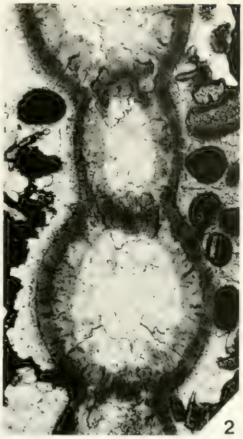
7. USNM 485785b: longitudinal section showing structure of walls and tabulae, ×40.

8. USNM 485779a: longitudinal section through corallum based on a stromatoporoid, ×5.

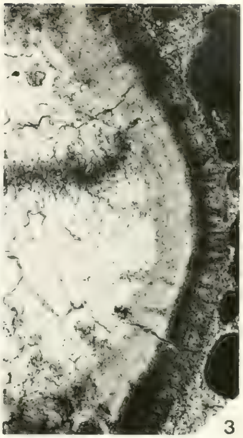
9–11. USNM 423421: 9, transverse section (note corallum of *Keelophyllum oklahomense* attached to ranks), ×8; 10, transverse section showing wall structure (detail from lower right in 9, turned 110° clockwise), ×40; 11, transverse section showing a tubule (detail from right of center in 9, turned 80° clockwise), ×40.



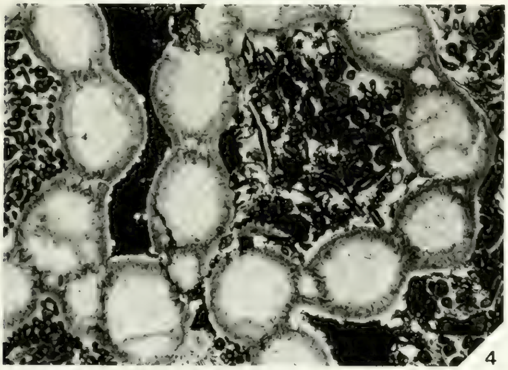
1



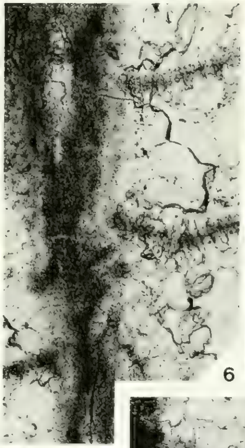
2



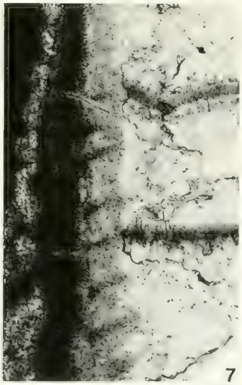
3



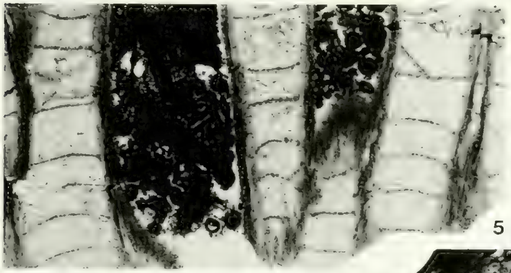
4



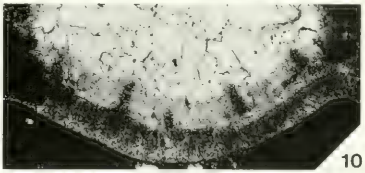
6



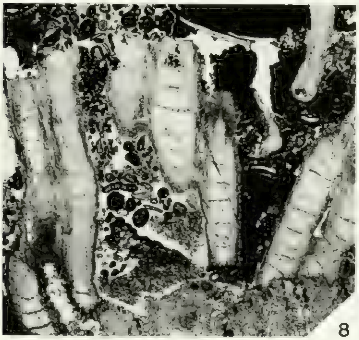
7



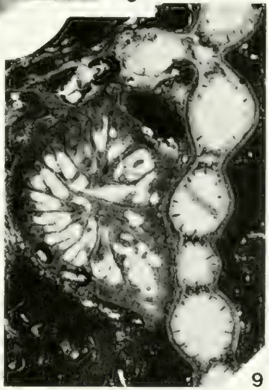
5



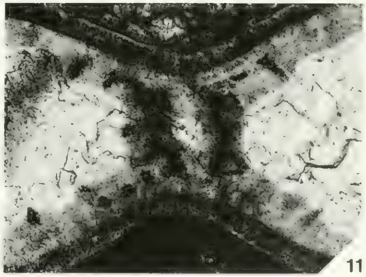
10



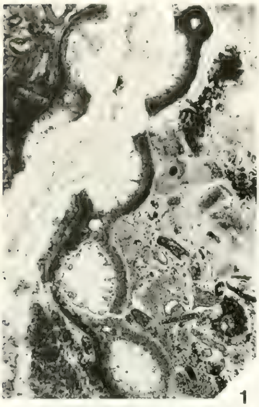
8

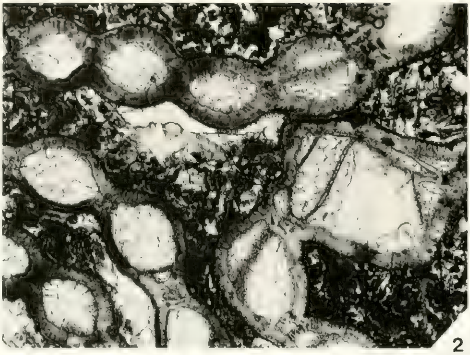


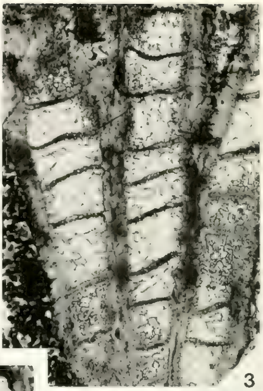
9

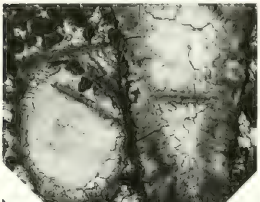


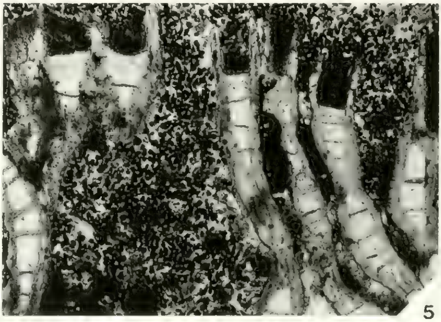
11

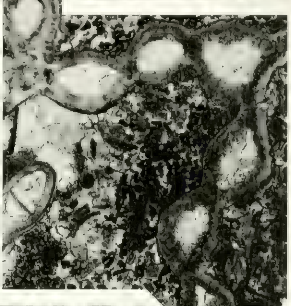

1

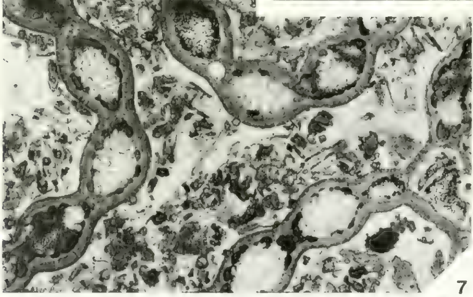

2

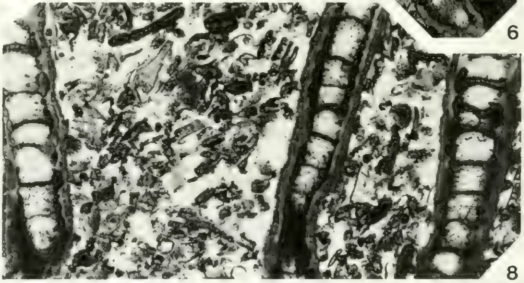

3

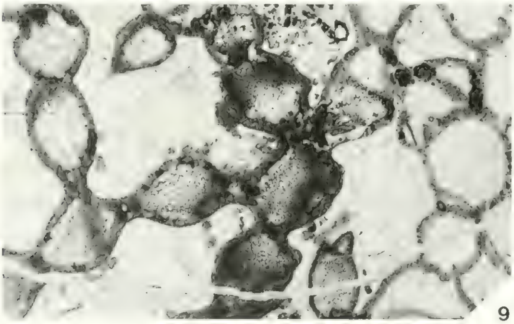

4

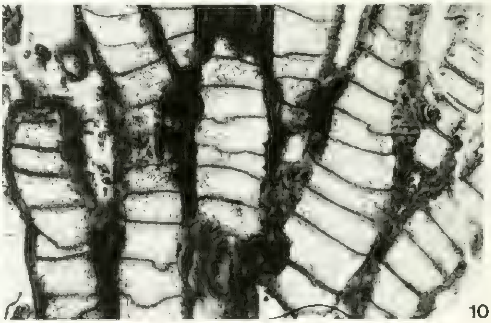

5


6


7


8


9


10

EXPLANATION OF PLATE 10

Figure | Page
1–10. ***Halysites alexandricus,*** new species 67

[1, Cason Shale, Section-interval 33-1 (Buffalo River); 2–6, Leemon Formation, Section-interval 31-1 (Thebes North); 7–10, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 15-1 (Calumet).]

1. USNM 485795: transverse section showing rank cut by a vein, ×8.

2–4. USNM 485781 (holotype): 2, transverse section showing "megacorallite" (right of center), ×8; 3, longitudinal section, ×8; 4, longitudinal section (note probable encrusting tentaculitid on left), ×15.

5, 6. USNM 485796: 5, longitudinal section showing calices, ×5; 6, transverse section, ×8.

7, 8. USNM 485783 (paratype): 7, transverse section, ×8; 8, longitudinal section, ×8.

9, 10. USNM 485800a: 9, transverse section (note irregularly shaped corallites on right side), ×8; 10, longitudinal section, ×8.

EXPLANATION OF PLATE 11

Figure Page

1–6. ***Halysites alexandricus,*** new species 67

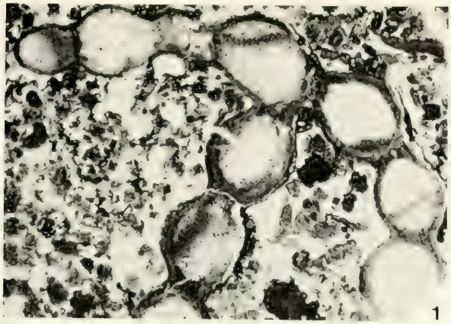
[1, 2, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 14-1 (Higginbotham Farm); 3, 4, Wilhelmi Formation, Section-interval 37-1 (Essex); 5, 6, Wilhelmi Formation, 3.2 km south of Channahon, Illinois.]

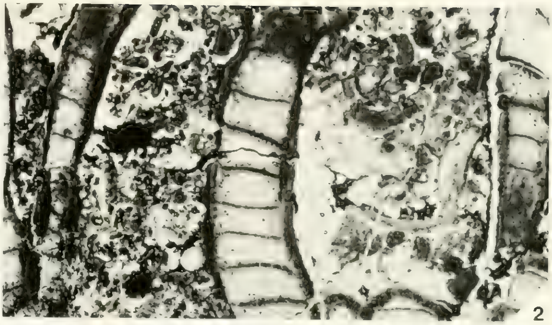
1, 2. USNM 485804: 1, transverse section, ×8; 2, longitudinal section, ×8.
3, 4. USNM 485809: 3, transverse section, ×8; 4, longitudinal section, ×8.
5, 6. UI X-8723 (paratype): 5, transverse section, ×8; 6, longitudinal section, ×8.

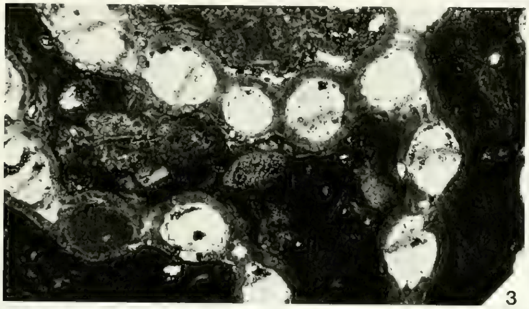
7–9. ***Halysites*** species cf. ***H. alexandricus,*** new species 72

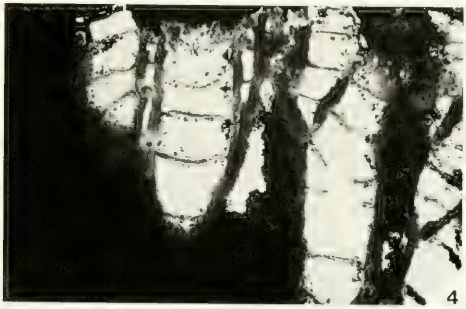
[7–9, Sexton Creek Limestone, Sexton Creek, Illinois.]

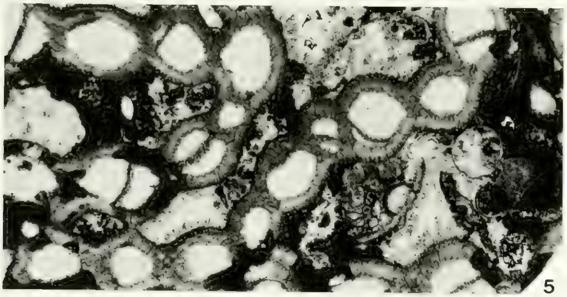
7–9. UI C-1346a: 7, transverse section, ×8; 8, transverse section, ×20; 9, longitudinal section, ×8.

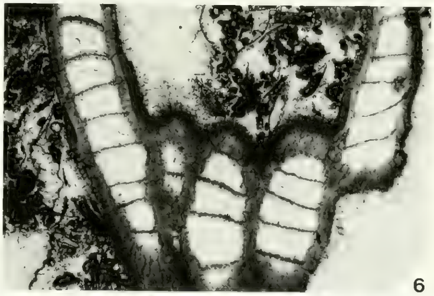

1

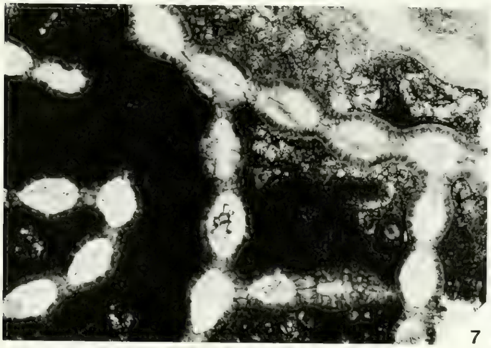

2

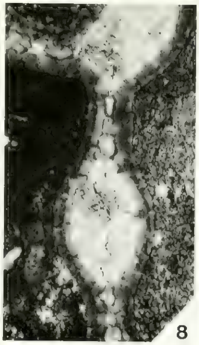

3

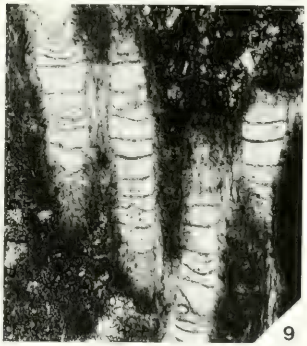

4

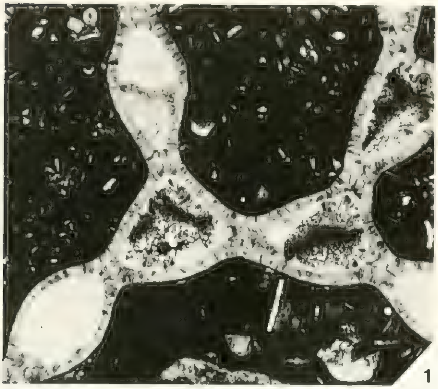

5

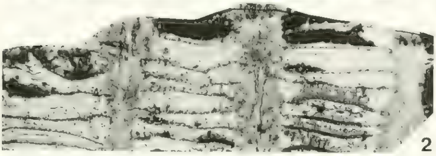

6

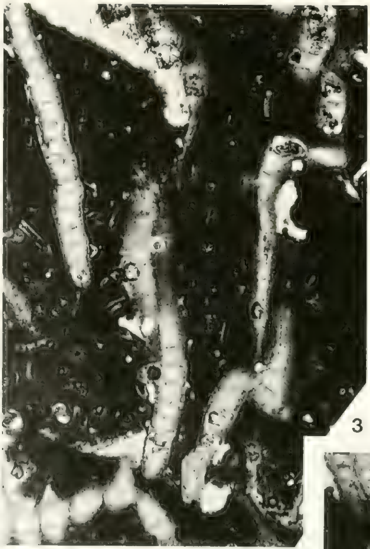

7

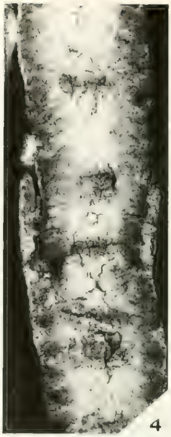

8

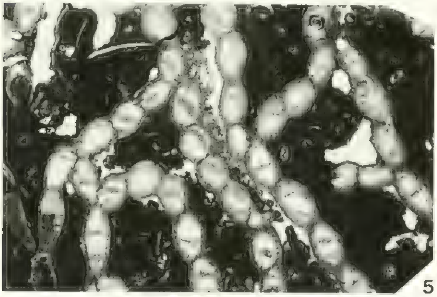

9

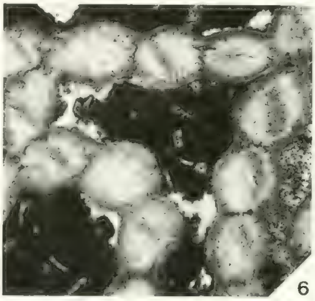

1

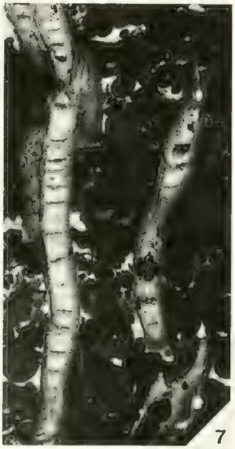

2

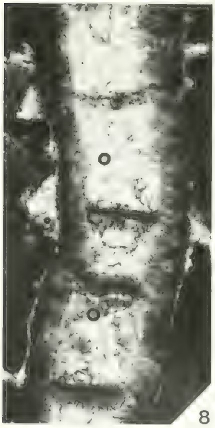

3

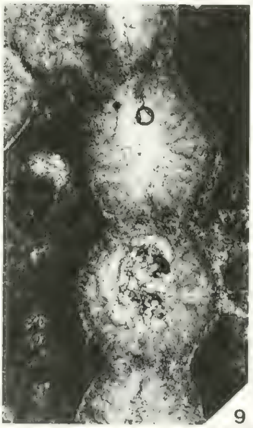

4

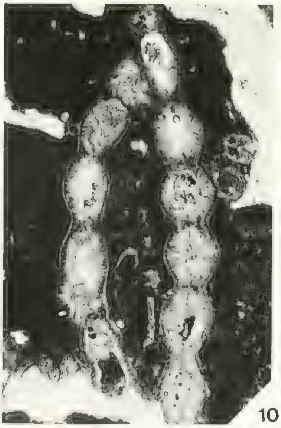

5

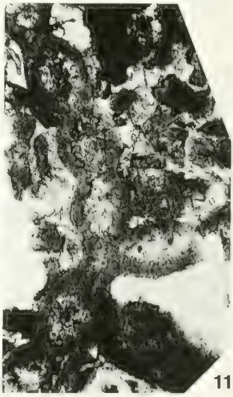

6


7


8


9


10


11

EXPLANATION OF PLATE 12

Figure		Page
1, 2.	***Halysites*?** species A	73
	[1, 2, Sexton Creek Limestone, Sexton Creek, Illinois.]	
	1, 2. UI C-1346b: 1, transverse section, ×8; 2, longitudinal section, ×8.	
3–11.	***Catenipora lawrencica*,** new species	74
	[3–10, *Brevilamnulella* beds, Keel Formation, Section-interval 23-2 (Lawrence Quarry) (site 23iv); 11, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 14-1 (Higginbotham Farm).]	
	3–6. USNM 485780b (holotype): 3, longitudinal section, ×8; 4, longitudinal section through a single corallite, showing rejuvenation (detail from upper left in 3, turned 10° clockwise), ×40; 5, transverse section, ×8; 6, transverse section (detail from left of center in 5, turned 40° clockwise), ×15.	
	7–10. USNM 485785c (paratype): 7, longitudinal section, ×8; 8, longitudinal section (detail from lower left of center in 7), ×40; 9, transverse section (detail from upper right of center in 10), ×40; 10, transverse section, ×15.	
	11. USNM 485812b (paratype): transverse section, ×15.	

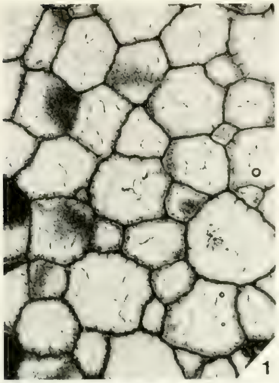
EXPLANATION OF PLATE 13

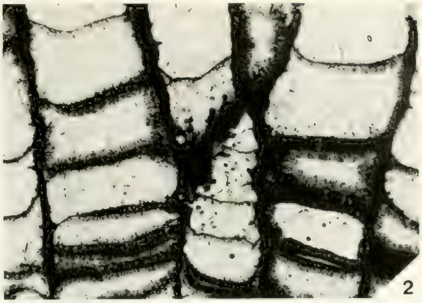
Figure Page

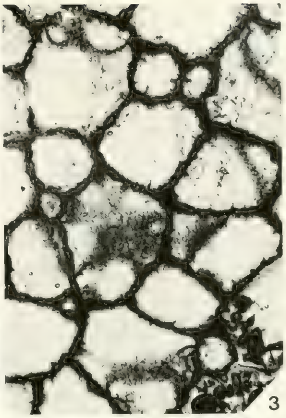
1–11. ***Paleofavosites subelongus*** (Savage, 1913) 78

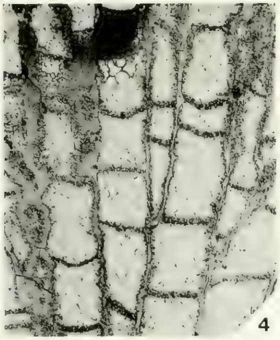
[1, *Brevilamnulella* beds, Keel Formation, Section-interval 23-2 (Lawrence Quarry) (site 23iv); 2, 3, oölite of Keel Formation, Section-interval 23-3 (Lawrence Quarry) (site 23i); 4, 5, Leemon Formation, Section-interval 31-1 (Thebes North); 6, 7, unnamed member, Bryant Knob Formation, Section-interval 18-1 (Kissenger); 8–11, Bryant Knob Formation (undivided), 5 km south of Clarksville, Missouri.]

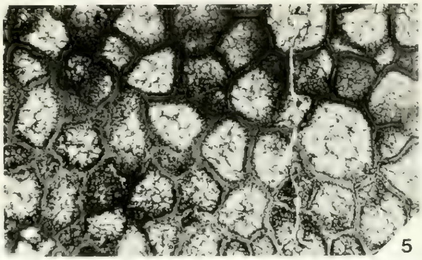
1. USNM 485785a: transverse section, ×8.
2, 3. USNM 458776: 2, longitudinal section, ×8; 3, transverse section, ×8.
4, 5. USNM 485819: 4, longitudinal section, ×8; 5, transverse section, ×8.
6, 7. USNM 485824: 6, transverse section, ×8; 7, longitudinal section, ×8.
8, 9. UI X-878a (holotype): 8, transverse section, ×8; 9, longitudinal section, ×8.
10, 11. UI C-1465a: 10, transverse section, ×8; 11, longitudinal section, ×8.

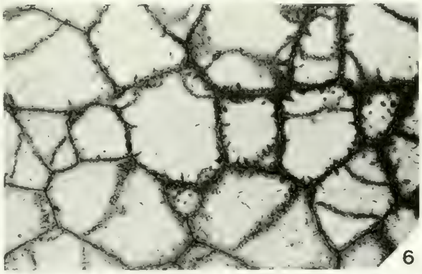

1

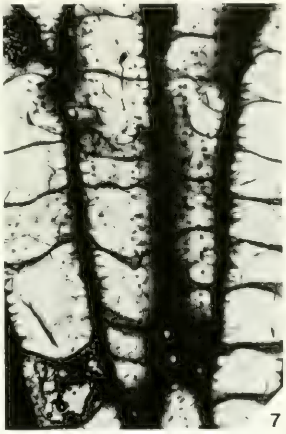

2

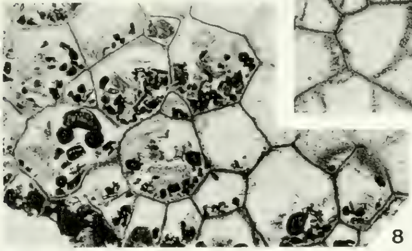

3

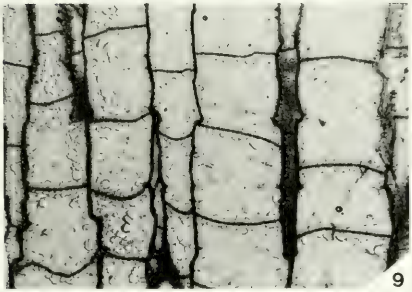

4

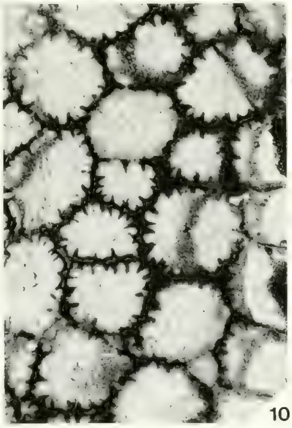

5

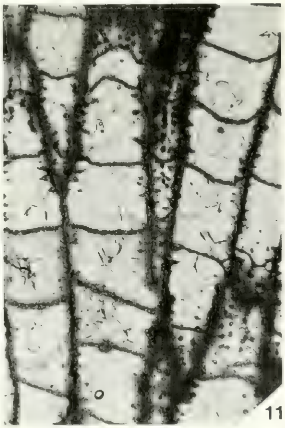

6

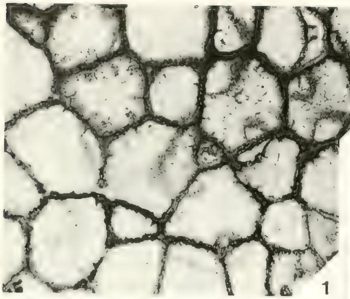

7

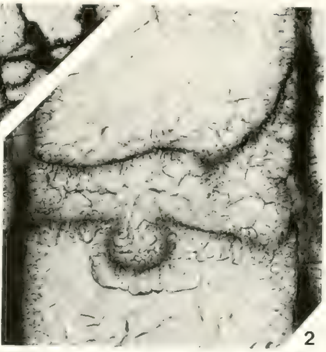

8

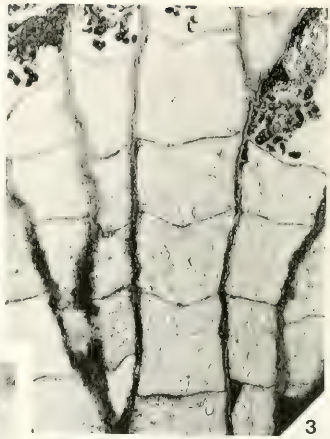

9

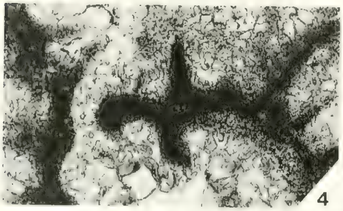

10

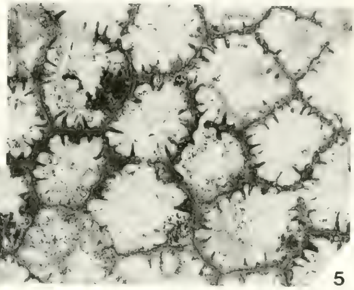

11

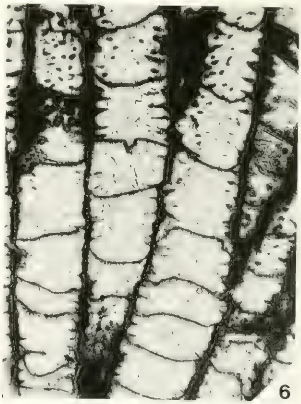

1

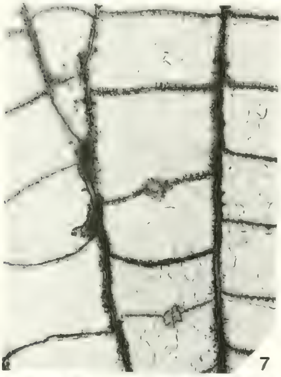

2

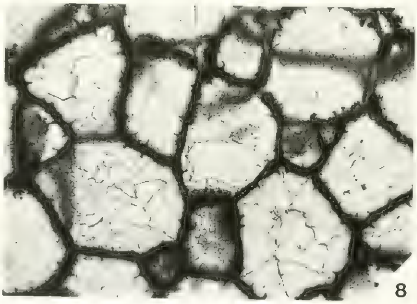

3

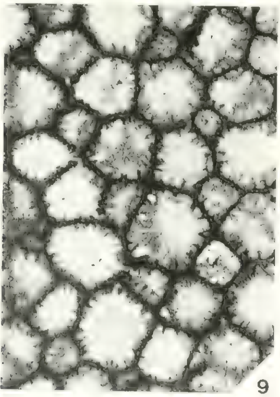

4

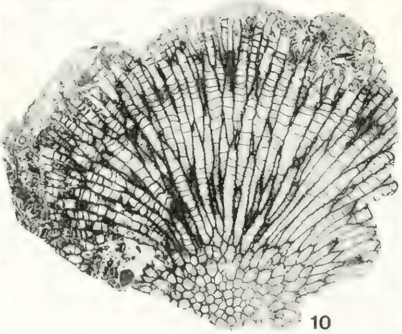

5

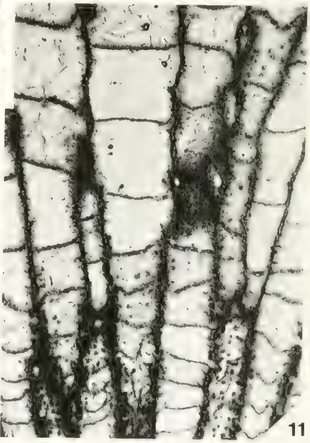

6


7


8


9


10


11

EXPLANATION OF PLATE 14

Figure Page

1–11. ***Paleofavosites subelongus*** (Savage, 1913) 78

[1–3, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 16-1 (Clinton Spring); 4–6, Bryant Knob Formation (undivided), Louisiana, Missouri; 7–11, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 15-1 (Calumet).]

1–3. USNM 459086: 1, transverse section, ×8; 2, longitudinal section through a corallite, showing lobe-like depression in tabula, ×20; 3, longitudinal section, ×8.

4–6. UI X-771: 4, transverse section showing septa and corner pore (detail from right of center in 5, turned 10° counterclockwise), ×40; 5, transverse section, ×8; 6, longitudinal section, ×8.

7, 8. USNM 485834: 7, longitudinal section, ×8; 8, transverse section, ×8.

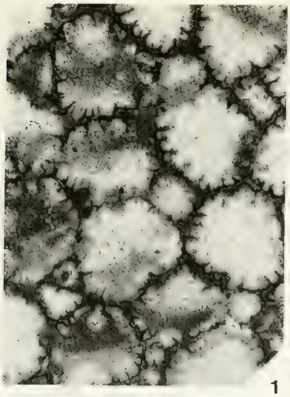
9–11. USNM 459074: 9, transverse section, ×8; 10, longitudinal section through entire corallum (note abrasion of upper surface), showing cyclomorphic variation and corallite expansion, ×1.5; 11, longitudinal section (detail from right of center in 10, turned 20° counterclockwise), ×8.

EXPLANATION OF PLATE 15

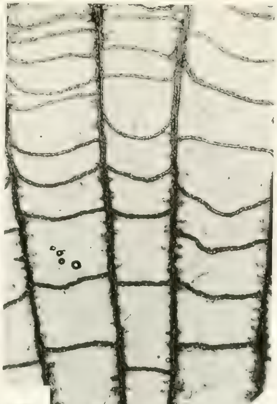
Figure		Page
1–12.	***Paleofavosites subelongus*** (Savage, 1913)	78

[1, 2, Cyrene Formation, near Edgewood, Missouri; 3–12, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 14-1 (Higginbotham Farm).]

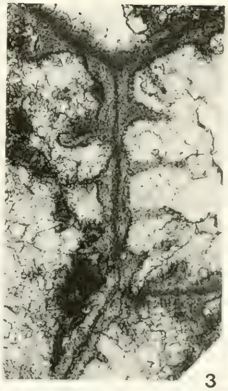
1, 2. UI C-1458d: 1, transverse section, ×8; 2, longitudinal section, ×8.
3. USNM 485850: transverse section showing structure of walls and septa, ×40.
4. USNM 485848: longitudinal section showing structure of wall and septa, ×40.
5–7. USNM 459080: 5, longitudinal section, ×8; 6, longitudinal section showing regeneration, ×8; 7, transverse section, ×8.
8, 9. USNM 459078: 8, transverse section, ×8; 9, longitudinal section, ×8.
10–12. USNM 459081: 10, longitudinal section, ×8; 11, transverse section through upper part of corallum, ×8; 12, transverse section from lower in corallum, ×8.



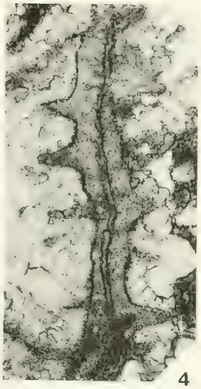
1



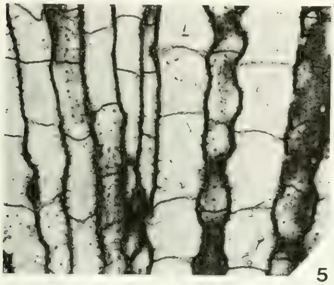
2



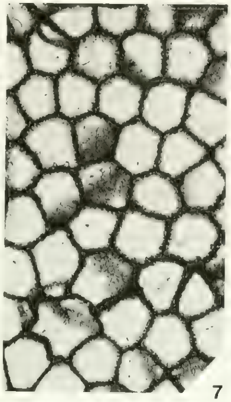
3



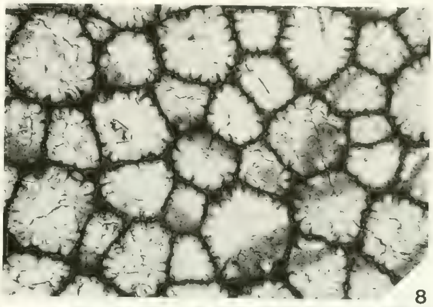
4



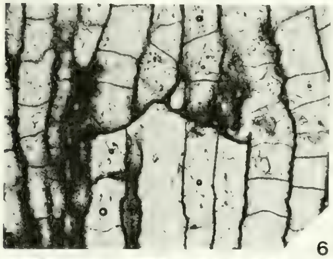
5



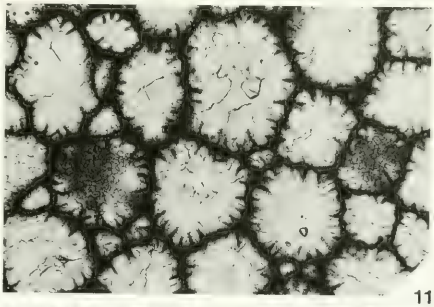
7



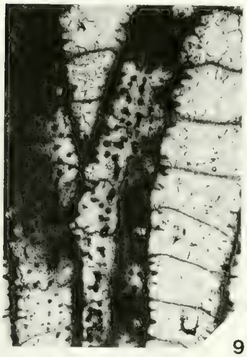
8



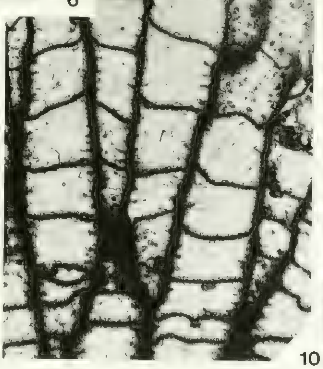
6



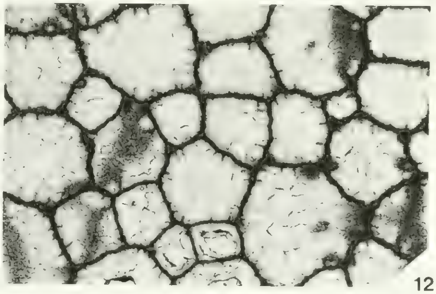
11



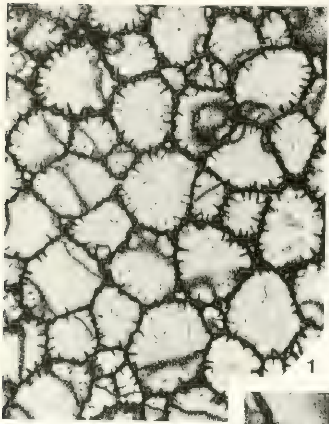
9

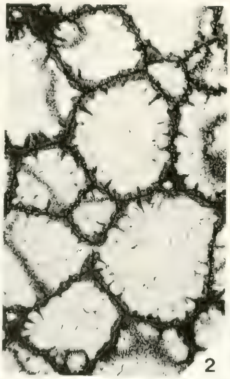


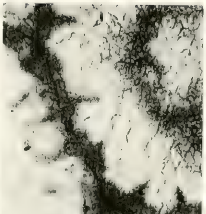
10

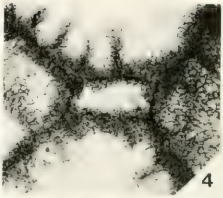


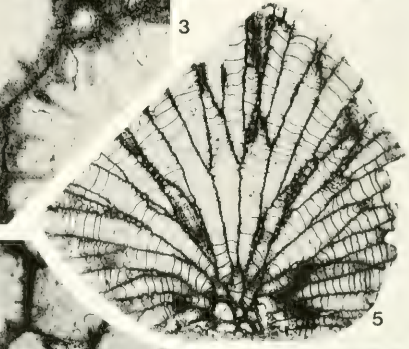
12

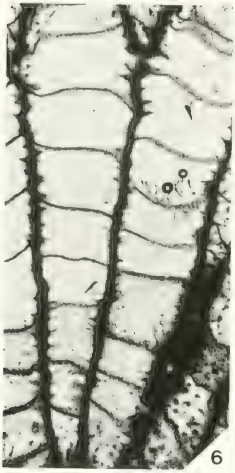

1

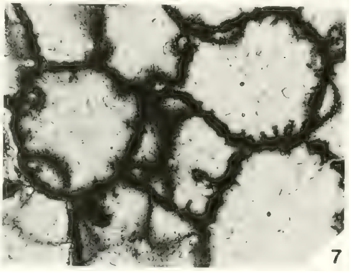

2

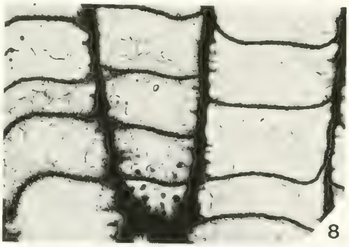

3

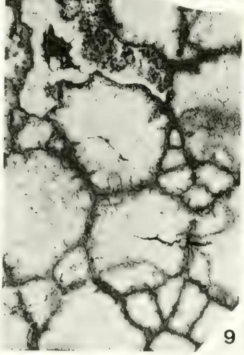

4

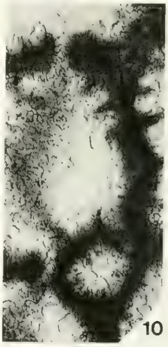

5

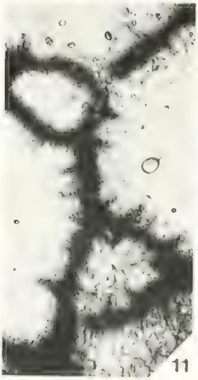

6

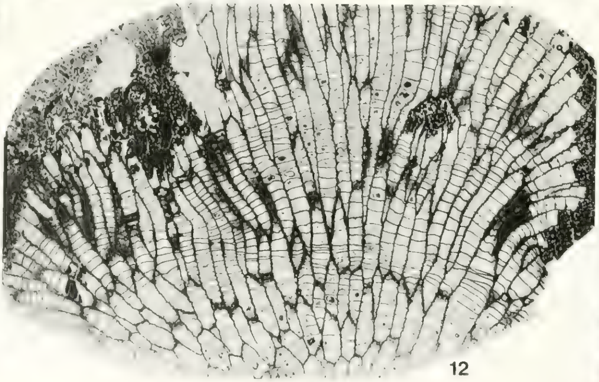

7

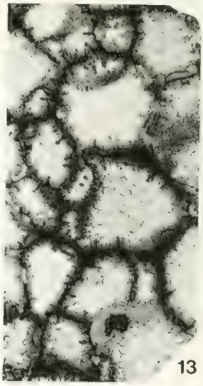

8


9


10


11


12


13

EXPLANATION OF PLATE 16

Figure Page

1–13. ***Paleofavosites subelongus*** (Savage, 1913) 78

[1–12, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 14-1 (Higginbotham Farm); 13, Cyrene Formation, Section-interval 13-0 (Bowling Green).]

1–6. USNM 459079: 1, transverse section, ×5; 2, transverse section (detail from upper left of center in 1), ×8; 3, transverse section showing three-sided offset (detail from right of center in 2, turned 30° counterclockwise), ×20; 4, transverse section showing four-sided offset, ×20; 5, longitudinal section through entire corallum, ×2; 6, longitudinal section (detail from center in 5, turned 10° clockwise), ×8.

7, 8. USNM 485866: 7, transverse section, ×8; 8, longitudinal section, ×8.

9. USNM 485839: transverse section showing regeneration following partial mortality, ×8.

10. USNM 485860: transverse section showing corner pore, mid-wall pore, and offset, ×20.

11. USNM 485846: transverse section showing offsets and corner pores, ×20.

12. USNM 485858c: longitudinal section through entire corallum (note abraded upper surface on left side), showing cyclomorphic variation in spacing of tabulae, ×1.5.

13. USNM 485874: transverse section, ×8.

EXPLANATION OF PLATE 17

Figure Page

1–7. ***Paleofavosites subelongus*** (Savage, 1913) 78

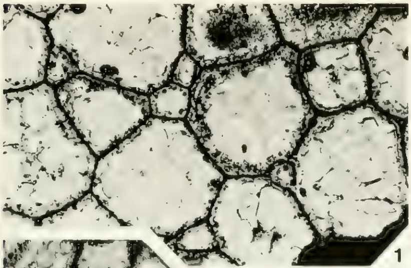
[1–3, Wilhelmi Formation, Section-interval 37-1 (Essex); 4–7, coral-rich bedding surface of Mosalem Formation, Section-interval 32-1z (Thomson East).]

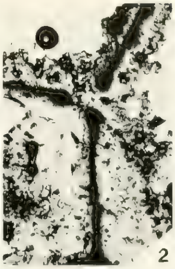
- 1–3. USNM 485877: 1, transverse section, ×8; 2, transverse section showing three-way corner pore, ×20; 3, longitudinal section, ×8.
- 4, 5. USNM 485886: 4, transverse section, ×8; 5, longitudinal section, ×8.
- 6, 7. USNM 485897: 6, transverse section ×8; 7, longitudinal section, ×8.

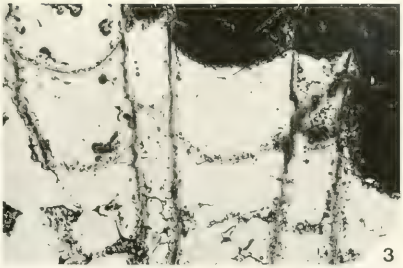
8–12. ***Paleofavosites*** species cf. ***P. subelongus*** (Savage, 1913) 89

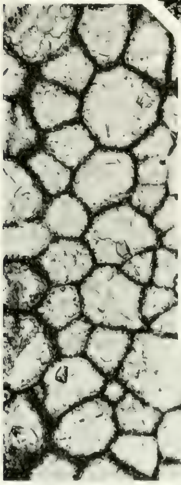
[8–12, upper Mosalem Formation, Section-interval 32-1c (Thomson East).]

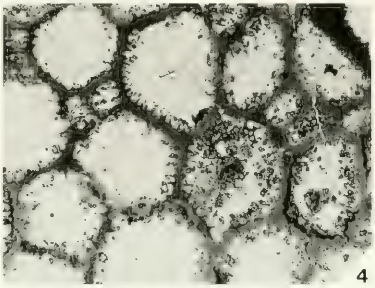
- 8. USNM 485930: transverse section showing mid-wall pore, ×20.
- 9, 10. USNM 485929: 9, transverse section, ×8; 10, longitudinal section, ×8.
- 11, 12. USNM 485934: 11, transverse section, ×8; 12, longitudinal section, ×8.

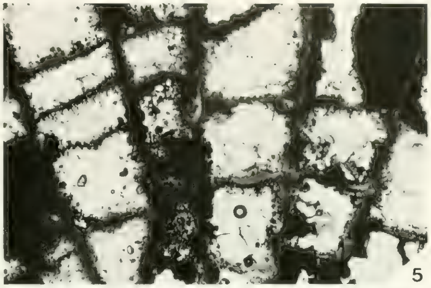

1

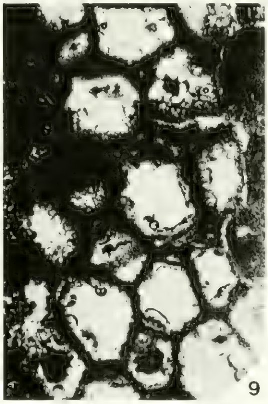

2

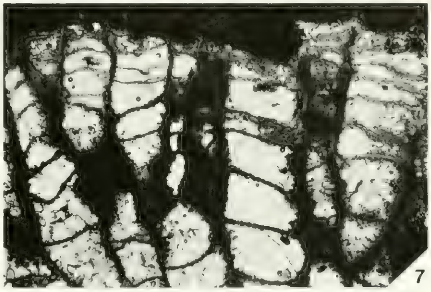

3

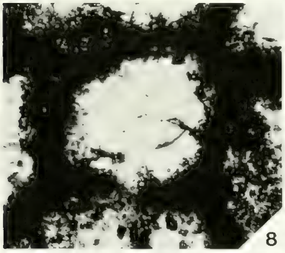

6

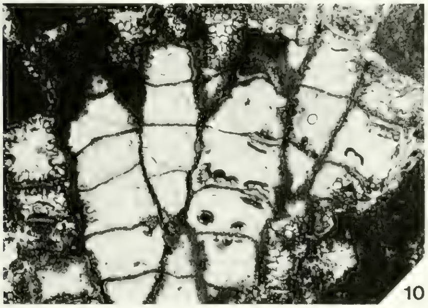

4

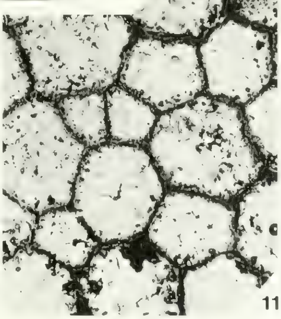

5

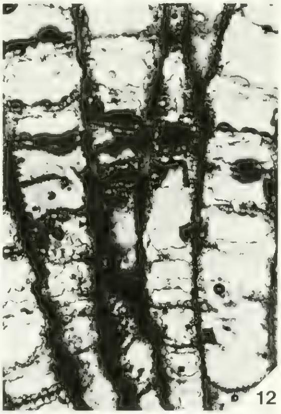

9

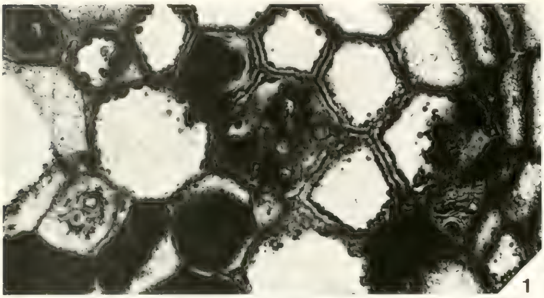

7

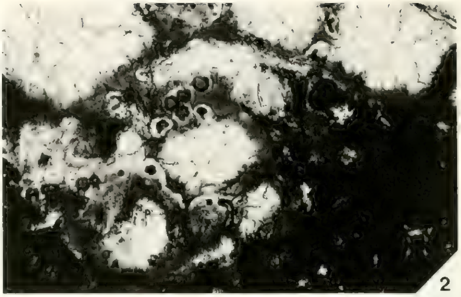

8

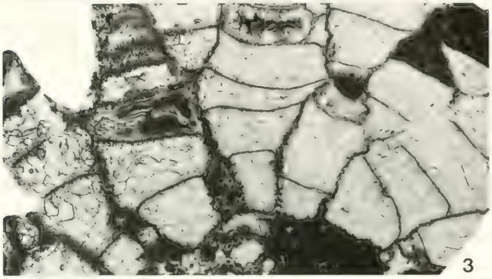

10

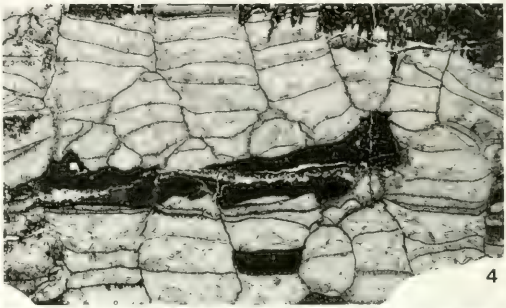

11

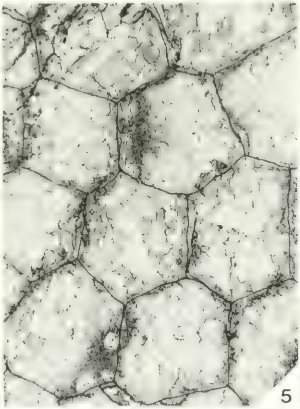

12

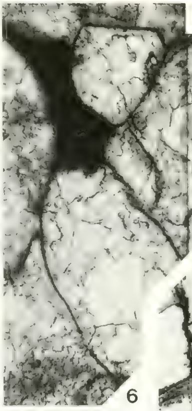

1

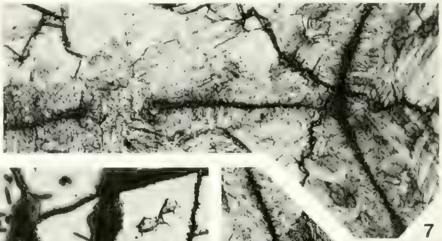

2

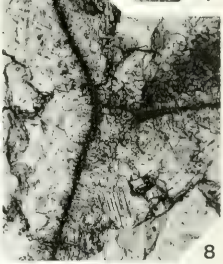

3

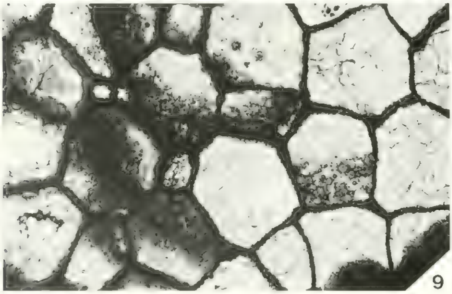

4

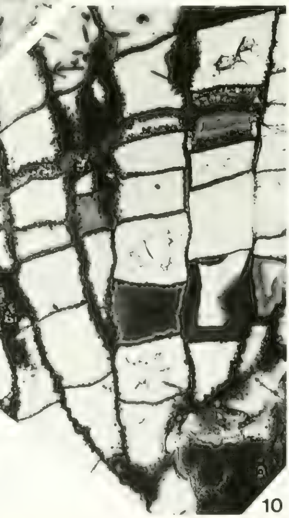

5

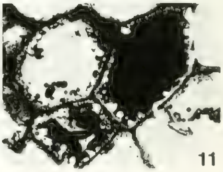

6


7


8


9


10


11

EXPLANATION OF PLATE 18

Figure		Page
1–11.	***Paleofavosites adaensis,*** new species	91

[1–3, Cochrane Formation, Section-interval 23-5 (Lawrence Quarry) (site 23i); 4–8, Cochrane Formation, Section-interval 35-1 (Henry House Falls); 9, 10, Sexton Creek Limestone, Alexander County, Illinois; 11, upper Mosalem Formation, Section-interval 10-3 (Lost Mound).]

1–3. USNM 485936 (holotype): 1, transverse section, ×5; 2, longitudinal section through base of corallum, showing group of basal corallites and holotheca, ×15; 3, longitudinal section, ×5.

4–8. USNM 485937 (paratype): 4, longitudinal section showing sediment inclusion and regeneration, ×5; 5, transverse section, ×5; 6, transverse section showing offsets produced during regeneration, ×15; 7, transverse section showing walls and mid-wall pore, ×40; 8, transverse section showing walls and corner pore, ×40.

9, 10. UI C-1347: 9, transverse section, ×5; 10, longitudinal section, ×5.

11. USNM 485941: transverse section, ×5.

EXPLANATION OF PLATE 19

Figure | Page
1–7. ***Paleofavosites*** species cf. ***P. ivanovi*** Sokolov, 1951a 94

[1–5, limestone facies at base of Bowling Green Dolomite, Section-interval 17-1a (Clarksville); 6, 7, Bowling Green Dolomite, Section-interval 36-1 (Indian Creek).]

1–5. USNM 485943: 1, transverse section, ×5; 2, transverse section of corallites at corallum margin, showing wall structure and curved free walls, ×20; 3, longitudinal section (note axial depressions in tabulae), ×8; 4, transverse section (detail from left of center in 1, turned 80° clockwise), ×8; 5, transverse section showing wall structure, ×40.

6, 7. USNM 485942: 6, longitudinal section, ×5; 7, transverse section, ×8.

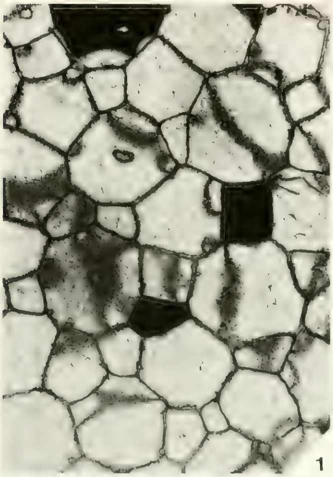
8–12. ***Paleofavosites*** species A 96

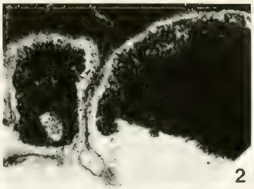
[8, Elwood Formation, Section-interval 5-2 (Schweizer North); 9–12, Elwood Formation, Section-interval 6-1 (Plaines West).]

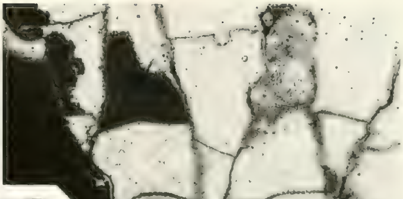
8. USNM 485944: exterior view of transverse surface (note crenulate tabulae), ×5.

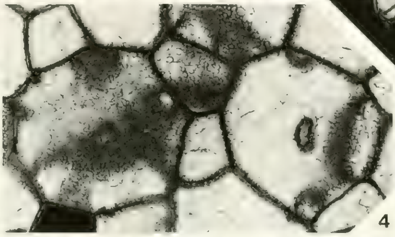
9, 10. USNM 485948: 9, transverse section, ×8; 10, longitudinal section, ×8.

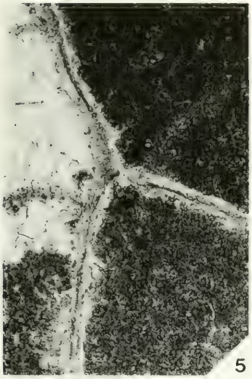
11, 12. USNM 485946: 11, transverse section, ×8; 12, longitudinal section showing cyclomorphic variation in spacing of tabulae, ×8.

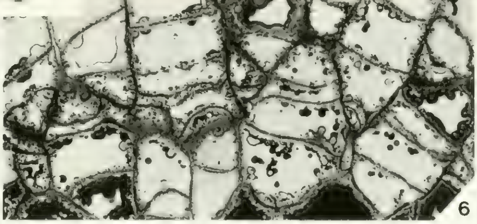

1

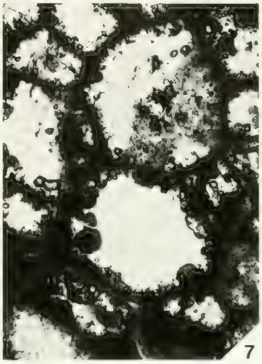

2

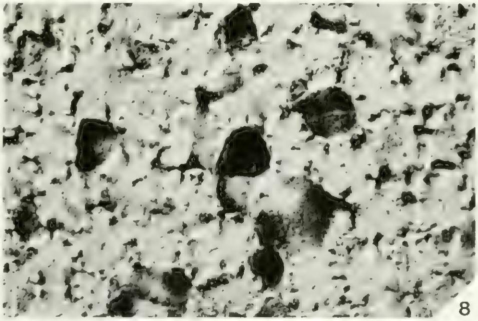

3

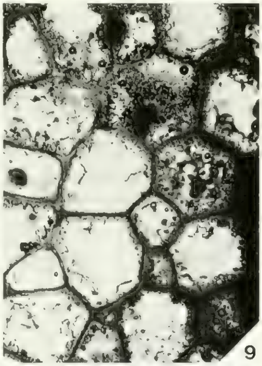

4

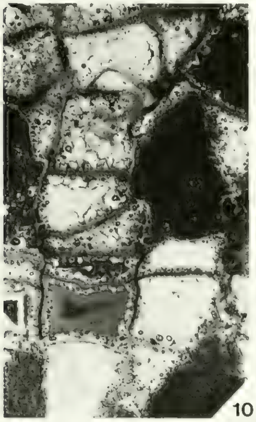

5

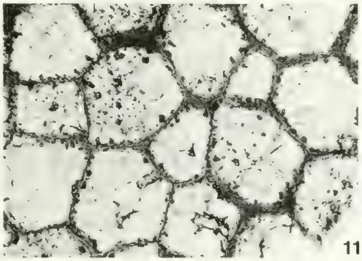

6

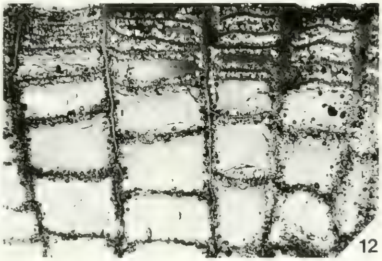

7

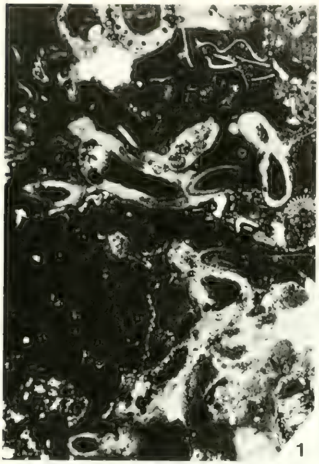

8

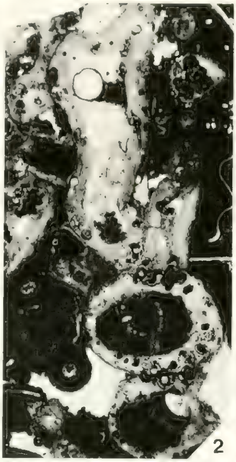

9

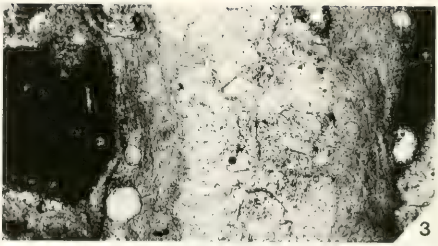

10

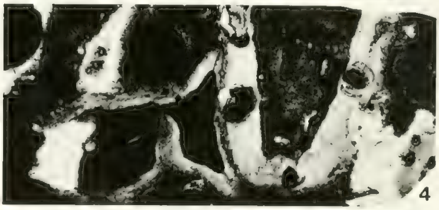

11

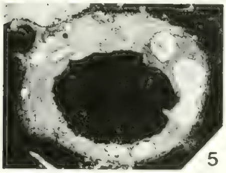

12

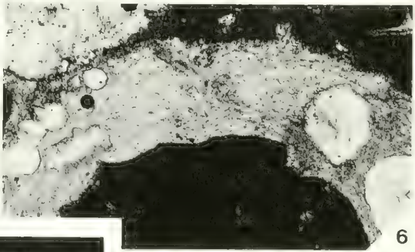

1

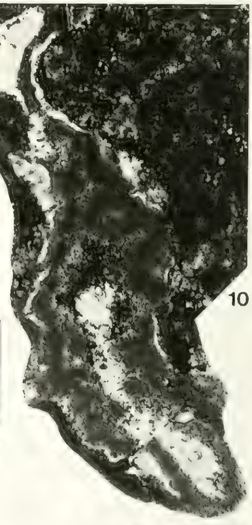

2

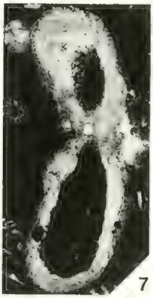

3

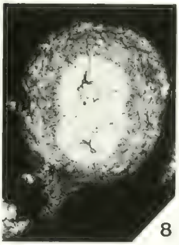

4

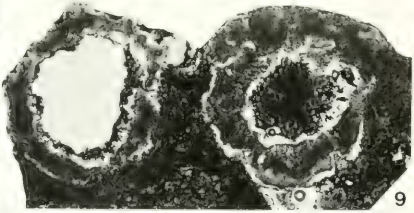

5

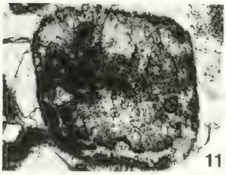

6

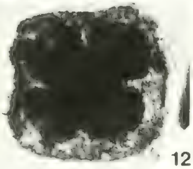

10

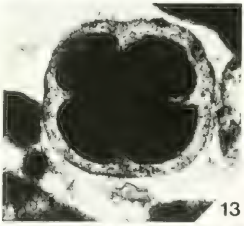

7

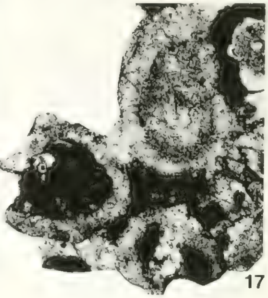

8

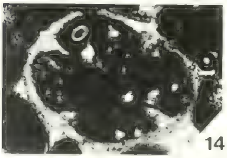

9

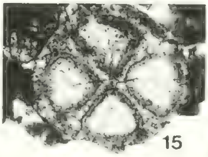

11

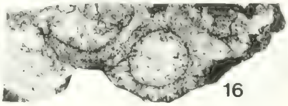

12


13


17


14


15


16

EXPLANATION OF PLATE 20

Figure | Page

1–10. ***Aulopora*** species A 97

[1–8, *Brevilamnulella* beds, Keel Formation, Section-interval 23-2 (Lawrence Quarry) (site 23iv); 9, 10, Wilhelmi Formation, Section-interval 37-1 (Essex).]

1–7. USNM 485785d: 1, transverse, oblique, and longitudinal sections of corallites (note that corallites encrust calcareous algae and one another), ×5; 2, two corallites (seen in longitudinal section) are based upon another corallite (in transverse section), and the corallite on the left has another corallite based upon it (on left), ×8; 3, longitudinal section of a corallite, with another corallite based upon it (on left; detail from above center in 2), ×40; 4, longitudinal section of a corallite, with another corallite based upon it (on left); 5, transverse section, ×15; 6, transverse section showing wall (detail from upper half in 5), ×40; 7, transverse oblique section of two connected corallites (detail from upper right of center in 1, turned 20° clockwise), ×15.

8. USNM 485780d: transverse section, ×40.

9, 10. USNM 485952: 9, transverse section, ×15; 10, longitudinal section of two connected corallites, ×15.

11–17. ***Rhabdotetradium*** species A 99

[11–13, Leemon Formation, Section-interval 20-3 (Short Farm); 14–17, Leemon Formation, Section-interval 31-1 (Thebes North).]

11–13. USNM 423401: serial transverse sections from a single corallite, in order from lowest to highest, ×40.

14. USNM 485770b: transverse section, ×40.

15–17. USNM 485953: serial transverse sections showing increase, ×40.

EXPLANATION OF PLATE 21

Figure Page

1–14. ***Palaeophyllum*** species 101

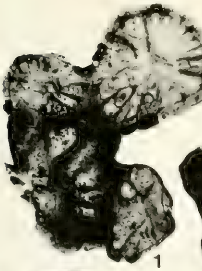
[1–3, oölite of Keel Formation, Section-interval 23-3 (Lawrence Quarry) (site 23i); 4, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 15-1 (Calumet); 5, 10–14, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 14-2 (Higginbotham Farm); 6–9, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 14-1 (Higginbotham Farm).]

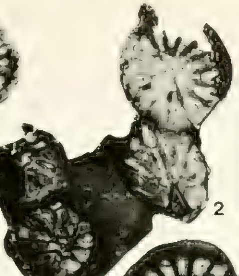
- 1–3. USNM 485954: serial transverse sections through a group of corallites, in order from lowest to highest, ×7.
- 4. USNM 485955: transverse section, ×7.
- 5. USNM 485959: transverse section, ×7.
- 6–9. USNM 485956: 6, 7, transverse sections, ×7; 8, transverse section showing structure of wall and septa (detail from upper half in 6, turned 20° clockwise), ×40; 9, longitudinal section, ×7; all from a single corallite.
- 10–12. USNM 485957: 10, 11, transverse sections, ×7; 12, longitudinal section, ×7; all from a single corallite (note epizoic bryozoan).
- 13, 14. USNM 485958: 13, transverse section, ×7; 14, longitudinal section, ×7; both from a single corallite.

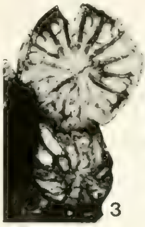
15–25. ***Pycnostylus*** species A 102

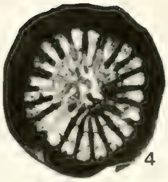
[15–25, channel-fill beds of Mosalem Formation, Section-interval 32-1b (Thomson East).]

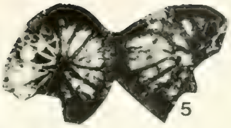
- 15–17. USNM 485960: 15, transverse section, ×15; 16, transverse section, ×4; 17, transverse section (detail from upper right side in 16, turned 20° clockwise), ×20.
- 18–22. USNM 485966: 18, exterior view of broken longitudinal surface, ×2; 19, longitudinal and oblique section, ×7; 20, transverse section showing connected corallites, ×15; 21, transverse section, ×7; 22, transverse section, ×7.
- 23–25. USNM 485961: 23, transverse section, ×7; 24, longitudinal section, ×7; 25, transverse section (detail from left side in 23), ×15.

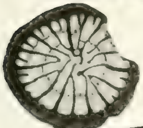

1

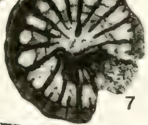

2

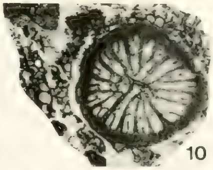

3

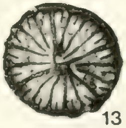

4

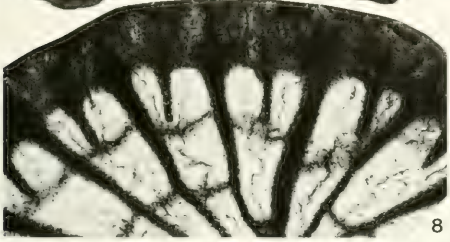

5

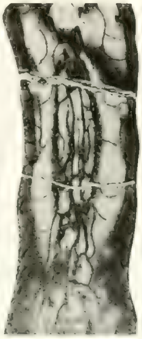

6

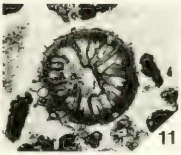

7

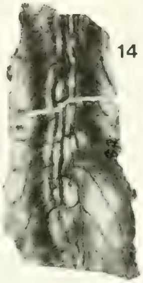

10

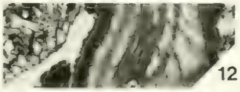

13

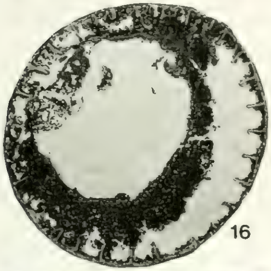

8

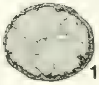

9

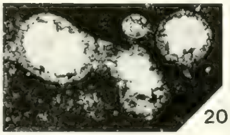

11

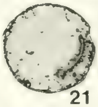

14

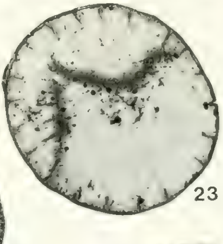

12

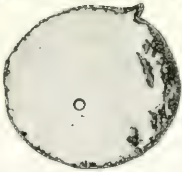

16

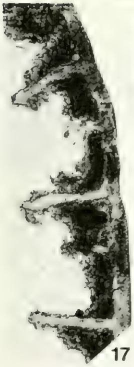

15

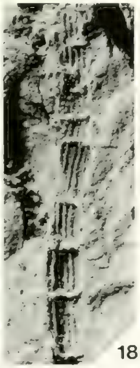

20

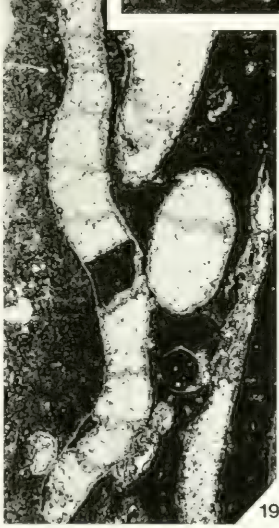

21

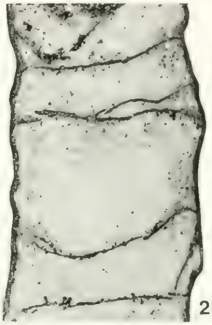

23

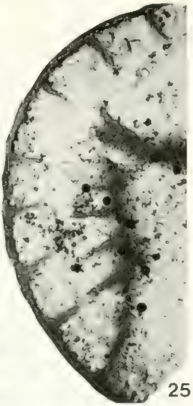

22


17


18


19


24


25

INDEX

Note: Page numbers are in light face; plate numbers are in **bold** face type; pages on which principal discussions occur are in *italics*; **F** and **B** indicate foldouts inside the front and back covers, respectively.

Aarhus (1982) 76
Abbott (1974) 24
Acanthohalysites Hamada 67
Acantholithus Lindstraam *65*
  lateseptatus Lindström 65
Acdalopora Bondarenko 44
Acervularia Davidsoni? Milne-Edwards and Haime 13
Acidolites Lang *et al.* *65*
  compactus Dixon 65
  sp. A **8**,11,17,18,*65*,**B**
  sp. Type 2 65
adaensis, Paleofavosites **18**,7,9–11,14,16,18,19,*40*,41,42,46,79,87,*91–94*,95
Adavere Stage 76,93,99
affinis,
  Heliolites 45,53,62
  Lyellia 45,54
  Propora 52–55,62
affinis (sp. aff.), *Propora* 7,14,15,18,47,52,*62*,**B**
Alabama 20
Aleman Formation 45
alexandricus, Halysites **9-11**,7,9–21,25,26,33,34,38, 41,46,66,*67*,*69–72*,73–75,97,123,**B**
alexandricus (sp. cf.), *Halysites* **11**,11,14,18,19,21,67,69,*72*,*73*,**B**
Allmon, W. D. 9
alveolaris, Palaeofavosites 95,96
Alyssites Fischer von Waldheim 67
americana,
  Lyellia 59,60,63
  Propora 45
Amsden (1957) 9,104
Amsden (1960) 9,25,104
Amsden (1961) 104
Amsden (1974) 8,13,19,21,34,104,105
Amsden (1980) 10
Amsden (1986) 8,19,21,25,27,104,105
Amsden (1988) 19
Amsden and Rowland (1965) 10
Anderson (1983) 106
Anse à Pierre-Loiselle Formation 64
Anstey (1986) 20
Anthozoa Ehrenberg 44
anticostiensis, Calapoecia 21
arctica, Catenipora 76
argutus, Palaeofavosites 96
Arkansas **F**,7,9,20
  Buffalo River 10,104
  Gilbert 10
  Marshall 10
  north-central 8
    eastern 10
    western **F**,*10*,17,18,34,72,104,**B**
  St. Clair Spring **F**,10
  Searcy Co. 10,72,104
Asia 75,76
asper, Paleofavosites 77
asper var. *maxima, Palaeofavosites* 93
aspera, Favosites 77
assueta, Aulopora 99
Athy (1928) 13,105
Atikameg Formation 54
Aulopora 75,*97*,98
  assueta Klaamann 99
  ellisensis Twenhofel 98
  enodis Klaamann 99
  serpens Goldfuss 97
  sp. 99
  sp. A **20**,9,10,13,15,17–19,26,33,*40*,*97–99*,**B**
  walliensis Webby 99
Aulopora (?) *trentonensis* Winchell and Schuchert 99
Auloporicae Milne-Edwards and Haime 17,97
Auloporida Sokolov 17,43,97
Auloporidae Milne-Edwards and Haime 17,97
Australasia 20
Australia, New South Wales 70,99,100
Aymestry Limestone 77

bacillifera, Propora 61
Bak and Elgershuizen (1976) 30
Baltic 75,76
Baltoscandia 61
Barannskiy Stage 76
Barnes (1988) 21,53,54,58,60,62,63,76,88,95,99,102
Barnes and Bolton (1988) 52
Barnes *et al.* (1981) 53
Barrick (1986) 8,18,19,104
Barrick *et al.* (1990) 104
Bassler (1950) 99,100
Becscie Formation 17,21,53,55,65,76
  member 1 21,87,89
Béland, J. E. 54
Bergström and Boucot (1988) 7,8,19
Berry and Boucot (1970) 18,63
Best *et al.* (1984) 42
Bighorn
  Dolomite 102
    Horseshoe Mountain Member 102
  Group 21
Billings (1858) 101
Billings (1865) 45,53,58–60,62,78,87,122
Billings (1866) 45,53,58,60,62,88,94
Binghamton University, Binghamton, New York 9
Birkhead (1967) 11,13,105
Birkhead, P. K. 9,13
Blake, D. B. 9
Blanding Formation 16,**B**
Bolton (1957) 45,52,53
Bolton (1979) 102
Bolton (1980) 45,52,54,58,59,61,88,93
Bolton (1981a) 20,45,53,54,58–60,62,63,65,76,78,87,88,94,95,99
Bolton (1981b) 64,93
Bolton, T. E. 9,52,53,76,77,87,88,95
Bolton and Nowlan (1979) 102
Bondarenko (1958) 44
Bondarenko (1963) 63
Bondarenko (1985) 34

- Bondarenko and Minzhin (1981) 59,61
- Bønsnes Formation 61
- Bowen Park
  - Group 70
  - Limestone 100
- Bowling Green Dolomite 12,13,19,94,96,105,134,**B**
- Brainard Shale 14–16
- Brassfield Formation 54,55,74,88
- Brenchley (1989) 8
- Brenchley *et al.* (1991) 8
- Brett *et al.* (1991) 52,93
- Brindle (1960) 21
- Bromide Formation 100
- Brown and Whitlow (1960) 20
- Bryant Knob Fm. 12,13,18,19,55,76,86,89,105,118,128,129,**B**
  - Kissenger Limestone Member 12,13,18,23,25–27,29–34,36,55,58,72,77,89,102, 105,118,119,121,125–127,129–131,136,**B**
  - unnamed member 12,13,18,25,26,33,89,128,**B**
- Buddemeier and Kinzie (1976) 32
- Buehler (1955) 71,73
- Bur Formation 95
- Burskiy Horizon 95

- *Calamopora* Goldfuss 39,77
- *Calapoecia* Billings 19,21,87
  - *anticostiensis* Billings 21
  - *favositoidea* Savage 11,13,78,87,89
- *Calopoecia favositoidea* Savage 89
- *Calvinia* Savage 44,45,60,61
  - *edgewoodensis* Savage 11,45,59,60–62
- Canada 20
  - Arctic, Somerset Island 71
- *cancellata, Propora* 54
- *cancellatiformis, Propora* 45,54
- Canomodine Limestone 70
- *capax,*
  - *Favosites* 88
  - *Palaeofavosites* 88
  - *Paleofavosites* 77,87,88,93–95
- *capax* (sp. cf.), *Paleofavosites* 88
- *capilliformis, Catenipora* 76
- Caramanica (1992) 102
- Cargo Creek Limestone 100
- Carter, J. G. 9,13
- Cason
  - "Brassfield" Limestone 10,**B**
  - Oölite 10
  - Shale 10,18,34,72,125,**B**
- Cataract Group, Manitoulin Formation 52
- *Catenipora* Lamarck 41,67,71,73,*74*,75,76
  - *arctica* Chernyshev 76
  - *capilliformis* Kokscharskaya 76
  - cf. *gotlandica* (Yabe) 74
  - *crassa* Stasinska 67
  - *escharoides* Lamarck 74,76
  - *gotlandica* (Yabe) 73,74
  - *jarviki* Stasinska 76
  - *lawrencica* n. sp. **12**,7,9,10,12,13,17,18,20,26,34,41,69,73,*74–76*,**B**
  - *minuta* Stasinska 76
  - n. sp. A 76
  - *panga* Klaamann 76
  - sp. 76
  - *zhejiangensis* Yü 76
- *Catenipora* (*Catenipora*?) *minima* Yü 76
- Cateniporinae Hamada 67
- *catenularia,*
  - *Halysites* 9,72
  - *Tubipora* 67
- *catenularia micropora, Halysites* 76
- *catenulata, Halysites* 13
- *catenulatus, Halysites* 11,13,72–74
- Caution Creek Formation 102
  - member 1 88
  - member 3 95,96
  - upper member 88,95,96
- *Cavella* Stechow 44,45,60
  - *edgewoodensis* (Savage) 59,60
- Cedar Lake Formation 54,103
- Channahon Limestone 55,72,89
- Chasm Creek Formation 87,88,102
  - member 1 88,95,96
  - member 2 88,95,96
- Chernyshev (1937) 93
- Chernyshev (1941) 74
- Chicotte Formation 53,54,63
- Chimneyhill Limestone
  - glauconitic member 9
  - oölitic member 9
- China 102
  - Chekiang Province 54,100
  - Guizhou Province 66
  - Jiangxi Province 76
  - Kiangsi Province 54,100
  - Zhejiang Province 76
- Churchill River Group 19
- Clear Creek Limestone 11
- Clemville Formation 93
- Cliefden Caves Limestone 99,100
- Coates (1984) 42
- Coccoserididae Kiaer 13,17,65
- *Coccoseris* Eichwald 65,66
- Cochrane Formation 9,10,19,94,133,**B**
- *Columnaria* sp? 13
- *compactus, Acidolites* 65
- *conferta,*
  - *Plasmopora* 61
  - *Propora* 45,52–55,58,62
- *conferta* var. *tunicata, Propora* 45,54
- Copper (1978) 93
- Cornulitidae Fisher 98
- Cote *et al.* (1968) 104
- County Route 2 105
- Craig (1984) 104
- Craig (1988) 104
- Craig, W. W. 8,9,72
- *crassa, Catenipora* 67
- *crassum, Rhabdotetradium jiangxiense* 100
- *cribriforme, Tetradium* 100
- Crooks, H. F. 8,72
- Cutter Dolomite 19
- *Cyathophylloides* Dybowski 19
  - *lyterion* Bolton 21
- *Cyathophyllum* sp? 13
- Cyrene Formation 12,13,18,20,33,39,55,58,65,86,89,105,123,130,131,**B**

- Dana (1846) 77
- *Davidsoni?, Acervularia* 13

Decorah Shale 99
Desmidopora Nicholson 78
Dixon (1974) 34,38,42,43,45,52,53,59–61
Dixon (1976) 68,71,72
Dixon (1986) 65
Dolbor Formation 99,100
Dolborskaya Horizon 99,100
Duncan, C. A. M. 9

East Arm Formation 54,88
Eckert (1988) 20
Edgewood
  Assemblage **F**,7–9,*14*,17–22,34,**B**
  Formation 11,13,55,58,62,65,72,89
    Cyrene Member 11
  Limestone 55,89
  Province **F**,7,8,*19–21*,22–26,29–31,33,34,36
edgewoodensis,
  Calvinia 11,45,59–62
  Cavella 59,60
  Heliolites? 11
Ehrenberg (1834) 44
Eichwald (1855–1860) 65
Elias (1982) 8,20,104,105
Elias (1989) 20,21,22
Elias (1991) 88,95,96,102
Elias (1992) 8,9,14,18,19,22,104–106
Elias and Young (1992) 8,14,19,21,45,58,64,72–74,76,78,94
Elias *et al.* (1988) 22
Elias, R. J. 8,9,44,72,77,100
Ellis Bay Formation 17,21,38,52,53,55,60–62,76,88,97,121
  member 2 60
  member 3 98
  member 5 76,88
  member 6 53,60,87
  member 7 53,60,65,99
ellisensis, Aulopora 98
Elwood Formation 14,15,17–19,63,97,105,122,134,**B**
Ely Springs Dolomite
  Floride Member 88
  Lost Canyon Member 88,102
England, southwest 40
enodis, Aulopora 99
Eocatenipora Hamada 74
Eolaminoplasma Bondarenko 63
escharoides, Catenipora 74,76
Essex Limestone 13
Estonia 17,61,70,74,76,87,93,99,100
  Borkholm 53,54,61
  Chavli 53
  Hohenholm in Dagö 61
  Island of Hiiuama 61
  Käargessaare 61
  Piersal 61
Europe 55
  northern 55
  northwestern 32
exigua, Propora 45,55

Favistina Flower 19
Favosites Lamarck 39,46,77,78,93,94
  aspera d'Orbigny 77
  capax Billings 88
  cf. *niagarensis* Hall 13
  cf. *venustus* of Savage 55
  favosus (Goldfuss) 9,11,94
  gothlandicus Lamarck 93,94
  ingens Klaamann 93
  niagarensis Hall 9,13
  prolificus Billings 87,88
  sp. 9,93
  sp? 13
  subelongus Savage 11,13,55,78,86,87,89
Favositicae Dana 17,18,77
favositid sp. indet. 14
Favositida Wedekind 17,18,22,25,41,43,77
Favositidae Dana 17,18,23,77
Favositina Wedekind 17,18,77
Favositinae Dana 17,18,42,77
favositoidea, Calapoecia 11,13,78,87,89
favositoidea, Calopoecia 89
favosus, Favosites 9,11,94
Fay (1988) 104
Fay (1989) 104
Fischer-Benzon (1871) 70
Fischer von Waldheim (1813) 67
Fischer von Waldheim (1828) 67
Fisher (1962) 98
Fisher Branch Formation 21,54
Flower (1961) 67,77,102
Flower and Duncan (1975) 44
Foerste (1909) 11,45,52,55,116–119
Foerste, A. F. 8,11,55
follis,
  Plasmopora 64
  Pseudoplasmopora 64
forbesiformis, Palaeofavosites 78,87
forbesiformis (sp. cf.), *Paleofavosites* 78,87
Fossil Hill Formation 93
Foster (1985) 42
Frech (1897) 44
Fritz (1937) 77
frutex, Rhabdotetradium 100

Gastropodenkalk 62
Geological Survey of Canada, Ottawa, Ontario 9,76
Germany
  Bensberg 97
  Eifel District 97
Gibson and Broadhead (1989) 29,31
Gierlowski and Langenheim (1985) 102
Girardeau Limestone 10,11,100,**B**
Girty (1895) 39
girvanensis, Propora (*Pinacopora*) 59,60
glabra, Propora 63
Goldfuss (1829) 77,97
Gondwana 8
gothlandicus, Favosites 93,94
gotlandica, Catenipora 73,74
gotlandica (cf.), *Catenipora* 74
gotlandicus, Halysites 73
gracile, Palaeophyllum 102
grayi, Pinacopora 59,60
Greenland 89
GSC [Geological Survey of Canada, Ottawa, Ontario, Canada] 44,52–54,60–62,87,88,95,97,99,121
Guelph Formation 102,103
guelphensis, Pycnostylus 102,103
guijangensis, Protaraea 66
Gun River Formation 52,53,62,87,88,95,96

Hall (1847) 65
Hall (1975) 70,77
Halysites Fischer von Waldheim 7,13,14,19–21,34,41,*67*,70,71,73,74
  alexandricus n. sp. **9-11**,7,9–21,25,26,33,34,38,41,46, 66,*67*,*69–72*,73–75,97,123,**B**
  catenularia (Linnaeus) 9,72
  catenularia micropora Whitfield 76
  catenulata (Linnaeus) 13
  catenulatus (Linnaeus) 11,13,72–74
  gotlandicus Yabe 73
  n. sp. A 72
  praecedens Webby and Semeniuk 70
  priscus Klaamann 70
  sp. 9,11,70
  sp. A 74
  sp. cf. *H. alexandricus* n. sp. **11**,11,14,18,19,21,67,69,*72*,*73*,**B**
  sp. cf. *H.* n. sp. A 73
  Halysites? sp. A **12**,11,18,19,67,69,*73*,*74*,**B**
  halysitid sp. indet. 12
  Halysitida Sokolov 17,18,25,41–44,*66*,*67*
  Halysitidae Milne-Edwards and Haime 17,18,67,74
  Halysitina Sokolov 44
  Halysitinae Milne-Edwards and Haime 67
  Ham (1973) 104
Hamada (1957) 67,74
Hamada (1959) 71
Harrington (1987) 23,24
Hawkins Limestone 9
Heliolites Dana 10,55
  affinis Billings 45,53,62
  sp. 11,13
  speciosus Billings 58,60
Heliolites? edgewoodensis of Savage 11
Heliolitida Frech 17,18,22,25,41–43,*44*,66,67
Heliolitina Frech 44
Hill (1959) 77
Hill (1981) 42,44,45,65–67,77,78,97,99,101,102
Hill and Stumm (1956) 77
Hodges and Roth (1986) 24
Högklint beds 73
Honorat Group 52,54
Hopkinton Dolomite 63
Hubbard and Pocock (1972) 30
Hubmann (1992) 34
Hudson River Group 87
Hunter (1985) 31
Hunton Group 104

Ideal Cement Company quarry 104
Illinois **F**,7,20
  Airport Road 105
  Alexander Co. 11,55,58,62,63,65,67,72–74,89,92,94,100,104,133
  Barber Greene Road 105
  Belvidere 15,105
  Boone Co. 15,105
  Calhoun Co. 12,96,105
  Carroll Co. 16,56,62,72,89,91,104,106
  Channahon 13,15,55,72,89,126
  Chicago 15
  Cortland 105
  DeKalb 15
  DeKalb Co. 15,63,105
  Des Plaines River valley 105
  Essex 15,105
  Gale 55,62,72,104
  Hamburg 105
  Horse Creek 105
  Indian Creek 105
  Jo Daviess Co. 16,94,105,106
  Johnson Creek 106
  Joliet 15
  Kankakee Co. 15,89,99,105
  Lost Mound 105
  McHenry Co. 15,105
  northeastern **F**,8,*13*,*14*,17–21,33,34,55,63,72,89,97,99,105,**B**
  northwestern **F**,*14*,16–19,33,34,55,62,72,89,91,94,104,105,**B**
  Savanna 16
  Schapville 106
  Sexton Creek 73,74,126,127
  southern **F**,8,*10*,*11*,14,17–19,34,45,55,58,61–63,65, 72–74,89,93,94,100,104,**B**
  Stockton 106
  Stone Quarry Road 105
  Thebes 55,58,62,63,65,104,123
  Thomson 106
  west-central **F**,*13*,17,19,34,94,96,104,**B**
  Will Co. 15,55,72,89,97,105
  Winston railroad tunnel 105
Illinois State Geological Survey, Champaign, Illinois 9
Indiana 19,20,63,88
ingens, *Favosites* 93
Interstate Route 35 104
Inwood Formation 88
Iowa **F**,20,63
  Bellevue 16
  Bellevue State Park 106
  Dubuque 16
  Dubuque Co. 16,105
  eastern **F**,*14*,16–18,20–22,33,105,**B**
  Jackson Co. 16,106
  King 105
Ivanov (1950) 96
ivanovi,
  Palaeofavosites 94,95
  Paleofavosites 21
ivanovi (sp. cf.), *Paleofavosites* **19**,12,13,18,19,21,79,87,89,*94*,*95*,**B**

Jaagarahu Stage 99
Jaani Stage 76
Jaanusson (1963) 54
Jaanusson and Mutvei (1982) 61
Jackson (1983) 23,25
jarviki, *Catenipora* 76
jiangxiense, *Rhabdotetradium* 100
jiangxiense crassum, *Rhabdotetradium* 100
Johnson and Lescinsky (1986) 21,54,88,102,103
Johnson *et al.* (1985) 18,21,22
Jones (1936) 94
Jupiter Formation 53,58,60,62,76,99
Juuru Stage 70,74,76,87,93

Kaljo *et al* (1988) 61
Kankakee Formation 12,15,72
  Drummond Member 105

  Offerman Member 105
  Troutman Member 105
Kanygin *et al.* (1988) 95,99,100
Keel Formation 9,10,18,19,23,25–27,34,53,55,58,66,72,76,77,89,98,99,102,104,117,120,124,128,136,**B**
  Brevilamnulella beds 9,10,22,23,25–27,29–34,36,55,66,72,77,89,99,116,117,123,124,127,128,135
  Ideal Quarry Member 9,10,89,104
  laminated calcilutite unit 10,33
Keelophyllum oklahomense McAuley and Elias 26,72,124
Ken-niho Conglomerate 54
Kentucky 19,20,63,88
Kershaw (1984) 23,24
Kershaw (1990) 24
Kiaer (1899) 61,65
Kiaer (1930) 54,61
Klaamann (1959) 93
Klaamann (1961) 76
Klaamann (1962) 93
Klaamann (1964) 77
Klaamann (1966) 70,74,76,99,100
Kluessendorf, J. 9
Kobluk *et al.* (1977) 23,24
Koenig *et al.* (1961) 105
Kokscharskaya in Volkova *et al.* (1978) 76,93
Korea, northwest 54
Koreanopora Ozaki 44
Kuranakhinskiy Horizon 93

La Vieille Formation 64
Lafuste and Tourneur (1988) 94
Lake Michigan 15
Lamarck (1816) 74
Lambe (1899) 45,53,59,60,64
Laminoplasma Bondarenko 63
Lang *et al.* (1940) 65,74,77
Lang River Formation 71
Langenheim, R. L., Jr. 9
Lasker (1980) 30
Laswell (1957) 105
lateseptatus, Acantholithus 65
Laub (1979) 45,54,67,74,77,88,89
Laufeld and Jeppsson (1976) 73,76
lawrencica, Catenipora **12**,7,9,10,12,13,17,18,20,26,34,41,69,73,*74–76*,**B**
Lee and Elias (1991) 34,71
Lee and Noble (1988) 38
Lee and Noble (1990) 33,88
Leemon Formation 10,11,18,20–23,25–27,29–34,36,45,55,58,62,65,72,89,100,104,117,118,120–123,125,128,135,**B**
leemonense, Streptelasma 26,72,100
Leleshus (1974) 45
Lemastus (1979) 10,104
Leptaena limestone 54
Lespérance *et al.* (1987) 54,58,61,88,93
Lespérance, P. J. 61
Liebe and Rexroad (1977) 105
Limestone Point Formation 64
Lin (1965) 66
Lin and Chow (1977) 54,76,100
Lindström (1899) 45,53,54,58–61,65
Linnaeus (1767) 67
logani, Plasmopora 64
logani (sp. cf.), *Plasmopora* **8**,13,17,18,20,*64*,**B**
Lonsdale (1839) 44,63
Louisville Limestone 63
Lowville Limestone 100
Ludvigson and Witzke (1988) 106
Lyellia Milne-Edwards and Haime 44
  affinis (Billings) 45,54
  americana Milne-Edwards and Haime 59,60,63
  cf. *thebesensis* (Foerste) 13
  sp. 11,13
  speciosa (Billings) 59,60
  thebensis Foerste 13
  thebesensis Foerste 9,11,13,45,52,55,58,65,89
    paucivesiculosa Bolton 45,52
Lyellia? sp? 13
lyterion, Cyathophylloides 21

magna, Propora 59,61
Magnesian Limestone 63
magnifica (cfr.), *Propora* 45,54
Maher and Lantz (1952) 10
Manistique Dolomite 63
Manitoba 20
  Hudson Bay Lowland 9,88,102
  northeastern 19
  northern 87,88,95,96,102
  southern 19,21,54,88,102,103
Manitoulin Formation 17,52,53,55
Manten (1971) 23,24,30,31
Maquoketa
  Group 15,16,20,21
  Shale 12,13
Matapédia Group, Grande Coupe beds 17,52,54,55,58,60–62
maxima (var.), *Palaeofavosites asper* 93
maximus, Palaeofavosites 93
Maxwell (1936) 9
McAuley and Elias (1990) 8–10,13,14,18–20,22,25,26,34,72,77,104–106
McAuley, R. J. 8,72,77,100
McCracken and Barnes (1982) 105
Mcleodea Flower and Duncan 44,45
Melchin *et al.* (1991) 53,60,65,87
Mesofavosites Sokolov 77,78
Mesosolenia Mironova 77,78
Michigan 63
micropora,
  Halysites catenularia 76
  Tetradium 100
Mikulic *et al.* (1985) 20,105
Miller (1889) 65,102
Milne-Edwards and Haime (1849) 44,63,67
Milne-Edwards and Haime (1850) 44,97,101
Milne-Edwards and Haime (1851) 44,45,53,59,62–65,77,97
minima, Catenipora (*Catenipora?*) 76
minimum, Palaeophyllum 102
Minnesota 99
minuta, Catenipora 76
Mironova (1960) 77
Mississippi
  River 104
    valley 105
Missouri F,7,20
  Blue Shawnee Creek 104
  Bowling Green 12
  Cape Girardeau 11,100
  Cape Girardeau Co. 11,58,72,100,104

  Clarksville 12,39,50,51,55,85–87,89,105,118,128
  Clinton Spring 105
  Edgewood 12,13,18,39,55,58,65,86,89,123,130
  Kissenger Hill 105
  Louisiana 12,86,89,105,129
  New Wells 104
  northeastern **F**,8,*13*,17–19,34,55,58,65,72,77,89,94,96,102,104
  eastern **B**
  western **B**
  Pike Co. 12,55,58,65,72,77,89,96,102,105
  southeastern **F**,8,*10*,*11*,17–19,21,34,58,72,100,104,**B**
  Stark Cemetery 105
Mongolia 17,61,62
Mosalem Formation 14,16,18–23,25–27,29–34,37,38,55,56,62,72,89,91,94,104,105,119,122,132,133,136,**B**
Mulde Marl 94
Multisolenia Fritz 77,78
multispinosa, Propora 54

n. sp., *Paleofavosites* 94
n. sp. A
  Catenipora 76
  Halysites 72
    sp. cf. *H.* 73
  Paleofavosites 94
Nabala Stage 61
National Museum of Natural History, Smithsonian Institution, Washingon, D.C. 9
Natural Sciences and Engineering Research Council of Canada 9
Nelson (1963) 77,78,88,95,96,102
Nevada 88
  Northern Egan Range 102
New Brunswick, northern 45,64
New Mexico 20
  southern 19
New York 65
niagarensis, Favosites 9,13
niagarensis (cf.), *Favosites* 13
Nicholson (1879) 99
Nicholson and Etheridge (1878) 44,59
Nicholson and Etheridge (1880) 59
nobile, Rhabdotetradium 99,100
Noble and Young (1984) 64
nodosus, Paleofavosites 89
Noix
  Limestone 12,13,105,**B**
  Oölite 13,34
Noixodontus girardeauensis (Satterfield) 18
North America 7–9,61,70,88,100,102
  central 20,75
  eastern 20,55,65,75
Northrop (1939) 64
Northwest Territories, Aberdeen Lake 102
Norway 27,95,96
  Asker district 93
  Herö 61
  Island of Heraay 61
  Malmaay 93
  Oslo region 76
  Ringerike 61,76,93
  Spirodden 93
  Stord 54,61
Novaya Zemlaya 93
Nowlan (1983) 93
Nutting (1900) 44

Oekentorp (1971) 77
Oekentorp (1976) 77
Oekentorp and Schouppé (1969) 78
oelaensis, Palaeofavosites 93
Offley Island Formation 89
Ohio 19,20,54,74,88
Oklahoma **F**,7,8,20,100
  Ada 10,91
  Ardmore 10
  Carter Co. 10,89,94,104
  Cedar Village 104
  Coal Co. 10,72,104
  Coal Creek 104
  Gobbler Knob 104
  Henry House Creek 104
  Henry House Falls 104
  Hickory Creek 104
  Lawrence 104
  Murray Co. 10,104
  northeastern 10
  Pontotoc Co. 10,55,58,66,72,74,77,89,94,99,102,104
  Qualls **F**,10
  south-central **F**,*9*,*10*,14,17–19,34,55,58,66,72,77,89,94,98,99,102,104,**B**
oklahomense,
  Keelophyllum 26,72,124
  Tetradium 100
Okulitch (1936) 99
Oliver (1968) 34,40,42,43
Oliver, W. A., Jr. 9
Ontario 20,63,102
  Bidwell Township 52
  Manitoulin Island 52,55,93
  Owen Sound 52,55
  southern 9,17,52
  southwestern 103
Oölitic Limestone 13
Orbigny, d' (1850) 77
Orchard Creek Shale 10,11,100
Ordovician–Silurian boundary 7,21
Owen (1844) 63
Owen *et al.* (1990) 61
Ozaki (1934) 44,45,54

Palaeofavosites
  alveolaris (Goldfuss) 95,96
  alveolaris (Lonsdale) 95,96
  argutus Ivanov 96
  asper var. *maxima* Chernyshev 93
  capax (Billings) 88
  forbesiformis Sokolov 78,87
  ivanovi Sokolov 94,95
  maximus Chernyshev 93
  oelaensis Klaamann 93
  prolificus (Billings) 78,88
  sinclairi Caramanica 102
  spiroddensis Stasinska 95
Palaeofavositinae Sokolov 77
Palaeohalysites Chernyshev 74
Palaeophyllum Billings 20,21,43,*101*,102
  gracile Flower 102
  minimum Yü 102

  pasense pasense Stearn 102
  raduguini Nelson 102
  rugosum Billings 101
  sinclairi Caramanica 102
  sp. **21**,9,10,12,13,17,18,25,34,*101*,*102*,**B**
  vaurealense Twenhofel 102
Paleofavosites Twenhofel 14,21,39,41,*77*,*78*,87,91,94
  adaensis n. sp. **18**,7,9–11,14,16,18,19,*40*,41,42,46,79,87,
    91–94,95,**B**
  asper (d'Orbigny) 77
  capax (Billings) 77,87,88,93–95
  ivanovi Sokolov 21
  n. sp. 94
  n. sp. A 94
  nodosus Poulsen 89
  prolificus (Billings) 77,87,88
  sp. 93
  sp. A **19**,14,15,18,41,46,79,87,89,*96*,97,**B**
  sp. cf. *P. capax* (Billings) 88
  sp. cf. *P. forbesiformis* Sokolov 78,87
  sp. cf. *P. ivanovi* Sokolov
    19,12,13,18,19,21,79,87,89,*94*,*95*,**B**
  sp. cf. *P. subelongus* (Savage)
    17,14,16,18,21,22,40,41,46,79,87,*89–91*,**B**
  sp. indet. 13,15,18
  subelongus (Savage) **13-17**,9–19,21,22,25,26,28–34,36,
    37,*38–40*,41,42,46,77,*78*,*79*,*81*,*82*,*84–89*,91,95,97,**B**
Paleofavosites (*Desmidopora*) 78
Paleofavositinae Sokolov 42,77
Paleontological Research Institution, Ithaca, New York 9
Paltodus dyscritus fauna 19
Pandolfi (1984) 30,31
Pandolfi (1985) 88,102
panga, Catenipora 76
Parakidograptus acuminatus Zone 18
parvistella, Stelliporella 32
pasense, Palaeophyllum pasense 102
pasense pasense, Palaeophyllum 102
paucivesiculosa,
  Lyellia thebesensis 45,52
  Propora thebesensis 52
Peabody Museum of Natural History, Yale University, New
    Haven, Connecticut 9,76
Pennsylvania 100
petalliformis, Porites 63
Petryk (1981) 76,88,98
Petryk, A. A. 99
Pettit Formation 10
Philcox (1971) 23,24,29,31
Philip (1960) 34
Pickerill and Harland (1984) 27
Pinacopora Nicholson and Etheridge 44
  grayi Nicholson and Etheridge 59,60
Pirgu Stage 61
Plasmopora Milne-Edwards and Haime 54,*63*,*64*
  conferta (Milne-Edwards and Haime) 61
  follis Milne-Edwards and Haime 64
  logani Young and Noble 64
  sp. A 64
  sp. cf. *P. logani* Young and Noble **8**,13,17,18,20,*64*,**B**
  thebesensis (Foerste) 11,62
Plasmoporidae Sardeson 17,20,63
Plattin Limestone 100
Platymerella manniensis zone 15,18,19,**B**
Počta (1902) 45
Poland 87
Poole, W. H. 54
Porites
  petalliformis Lonsdale 63
  tubulata Lonsdale 44
  vetustus Hall 65
Porkuni Stage 17,61,100
Potter *et al.* (1980) 25
Poulsen (1941) 77,89
Powell and Scrutton (1978) 77,78
praecedens, Halysites 70
Priscosolenia Sokolov 77,78
priscus, Halysites 70
prolificus,
  Favosites 87,88
  Palaeofavosites 78,88
  Paleofavosites 77,87,88
Propora Milne-Edwards and Haime
    13,14,19–21,41,*44*,*45*,52,53,56,59,63
  affinis (Billings) 52–55,62
  americana (Milne-Edwards and Haime) 45
  bacillifera Lindström 61
  cancellata Lindström 54
  cancellatiformis Sokolov 45,54
  cfr. *magnifica* Počta 45,54
  conferta Milne-Edwards and Haime 45,52–55,58,62
    var. *tunicata* Sokolov 45,54
  exigua (Billings) 45,55
  glabra Owen 63
  magna Sokolov 59,61
  multispinosa Lin and Chow 54
  n. sp. aff. *P. thebesensis* (Foerste) 58
  savagei n. sp. **5**,**6**,7,9–13,17,18,20,34,*35*,41,42,
    46,47,52,*56–58*,61,**B**
  sp. A **8**,11,18,19,27,45,47,*63*,**B**
    sp. A of Bolton 52,54
  sp. aff. *P. affinis* (Billings) **7**,14,15,18,47,52,*62*,**B**
  sp. aff. *P. speciosa* (Billings) 58,60
  speciosa (Billings)
    6,**7**,11,14,16–18,20,22,*38*,41,42,45,47,*58–62*,**B**
  thebesensis (Foerste) **1-4**,9–14,16–20,22,25,28–34,
    35,36–38,41,42,*45–48*,*50–56*,58,62,64,85,**B**
  paucivesiculosa (Bolton) 52
  tubulata (Lonsdale) 55
  yabei Ozaki 45,54
Propora (*Pinacopora*) *girvanensis* (Nicholson and Etheridge)
    59,60
Proporidae Sokolov 17,18,23,35,44,45
Protaraea Milne-Edwards and Haime *65*,*66*
  guijangensis Lin 66
  sp. A **8**,9,10,17,18,25,26,*66*,**B**
Pryor and Ross (1962) 104
Pseudoplasmopora follis (Milne-Edwards and Haime) 64
Pycnostylidae Stumm 17,20,102
Pycnostylus Whiteaves 20,*102*
  guelphensis Whiteaves 102,103
  sp. A **21**,14,16–18,20,33,*102*,*103*,**B**
Pycnostylus? sp. 14

Québec 20
  Anticosti Island 7,9,17,20,21,38,52–55,58,60–63,65,76,
    77,87–89,95–99,102,121
  Carleton 52,54
  Ellis Bay 62
  Gaspé Peninsula 9,17,64,93

  Grande Coupe 54,61
  Junction Cliff 53,60
  Jupiter River 53
  Lac St.-Jean 101
  Little Discharge 101
  Percé 52,54,55,58,60–62,88,93
  Petite Coupe 61
  Pointe Laframboise 52,99
  White Cliff 62,121
Queenston Delta Complex 20
Quepora Sinclair 74
Quondong Limestone 100

raduguini, Palaeophyllum 102
randi, Salvadorea 8
Reeds (1911) 9
Reedy Creek Limestone 100
Regan's Creek Limestone 100
Rhabdotetradium Sokolov *99*
  frutex Klaamann 100
  jiangxiense Lin and Chow 100
   crassum Lin and Chow 100
  nobile Sokolov 99,100
  sp. A **20**,11,17,18,20,*99*,*100*,**B**
  syringoporoides (Ulrich) 100
Richardson, J. 53
Richmondian Stage 19
Röda Lagret 61
ROM [Royal Ontario Museum, Toronto, Ontario, Canada] 44,52
   Rõõmusoks (1960) 53,54,61
Rose (1967) 106
Ross (1962) 18,105
Ross (1964) 18,106
Rotalites Leleshus 45
Rowley (1908) 13
Royal Ontario Museum, Toronto, Ontario 9
Rubey (1952) 13,105
Rugosa Milne-Edwards and Haime 8,17,101,**B**
rugosum, Palaeophyllum 101
Russia
  Arctic 74
  Siberian region 76
  Taimyr 76
  Verkhoyan 76
Rytteråker Formation 76

Salvadorea randi (Elias) 8
Sarcinulida Sokolov 19
Sardeson (1896) 63
Satterfield (1971) 104
Savage (1910) 11,104
Savage (1912) 13,105
Savage (1913) 11,13,44,45,52,59,60,78,86,87,89,104,105,128–132
Savage (1914) 13
Savage (1917) 11,13,45,52,59,78,86,87,89,104,105
Savage (1926) 105,106
Savage, T. E. 8,9,11,13,55,56,58,62,63,65,72–74,87,89,94
savagei, Propora **5**,**6**,7,9–13,17,18,20,34,*35*,41,42,46,47,52,*56–58*,61,**B**
Schedohalysites Hamada 67
Schouppé and Oekentorp (1974) 77,83
Scleractinia Bourne 42
Scotese and McKerrow (1990) 8,20
Scrutton (1975) 77
Scrutton (1983) 34
Scrutton (1985) 45,67,77
Scrutton (1987) 78
Scrutton (1989) 31,34,38,40–43
Scrutton (1990) 34,40,98
Scrutton (1993) 55
Scrutton and McCurry (1987) 55
Scrutton and Powell (1980) 34,39
Second Value Formation 102
Section
  3 (Garden Prairie) 14,15,33,*105*
  4 (Schweizer West) 13,15,18,19,*105*
  5 (Schweizer North) 15,18,97,*105*
  6 (Plaines West) 15,97,*105*
  8 (King) 14,16,*105*
  9 (Winston) 14,16,*105*
  10 (Lost Mound) 14,16,94,*105*
  11 (Schapville) 14,16,*105*
  12 (Stockton) 14,16,*106*
  13 (Bowling Green) 12,13,33,89,*104*
  14 (Higginbotham Farm) 12,13,23,25–27,29–34,55,58,72,76,77,89,102,*105*
  15 (Calumet) 12,23,25–27,29–34,55,70,72,89,102,*105*
  16 (Clinton Spring) 12,55,89,*105*
  17 (Clarksville) 12,96,*105*
  18 (Kissenger) 12,25,26,33,55,72,89,*105*
  19 (New Wells) 11,21,33,*104*
  20 (Short Farm) 11,33,34,38,42,58,72,100,*104*
  21 (Rock Crossing) 10,19,89,*104*
  22 (Cedar Village) 9,10,*104*
  23 (Lawrence Quarry) 10,19,22,23,25–27,29,31,32,34,35,53,55,58,66,70,72–74,76,77,89,94,97–99,102,*104*
  24 (Coal Creek) 10,25,33,34,72,*104*
  25 (Hunton) 10,34,72,*104*
  26 (Bellevue) 14,16,18,*106*
  29 (Sears Pit) 15,63,*105*
  30 (Thomson Northeast) 14,16,*106*
  31 (Thebes North) 10,11,23,25–27,29–34,38,52,55,58,62,65,67,72,89,100,*104*,117,118,120,121,123
  32 (Thomson East) 14,16,22–27,29,31,33,34,38,56,62,72,89,91,104,*106*
  33 (Buffalo River) 10,34,72,*104*
  34 (Belvidere South) 14,15,*105*
  35 (Henry House Falls) 10,19,94,*104*
  36 (Indian Creek) 12,96,*105*
  37 (Essex) 13,15,33,72,89,98,99,*105*
  Ch4 10
  Gale 11,38,45,50,51,55,60,62,72,*104*,122
Sepkoski (1986) 8
Series 6 95,96
serpens, Aulopora 97
Sexton Creek Limestone 11,19,45,55,63,72–74,93,94,123,126,127,133,**B**
Sheehan (1973) 20
Sheehan (1988) 8
Shimizu *et al.* (1934) 54
Shrock and Twenhofel (1953) 102
Siberia 39
  Tunguska 54
  Verkhoyan 93
Siberian Platform 21,74,95,96,99,100
Silurian assemblage 7,8,*14*,17–19,*21*,*22*,**B**
Simpson *et al.* (1960) 41
Sinclair (1955) 74
Sinclair, G. W. 54,61

- *sinclairi, Palaeophyllum* 102
- Skidmore and Lespérance (1981) 88,93
- Slite Beds 61
- Sloan (1987) 99
- Slovik Formation 93
- Sokolov (1947) 66,97
- Sokolov (1949) 44
- Sokolov (1950a) 77
- Sokolov (1950b) 45,54,77
- Sokolov (1951a) 77,94,95,134
- Sokolov (1951b) 77,78,87
- Sokolov (1955) 59,61,66,77,99,100
- Sokolov (1962) 59,61,77
- Sokolov and Tesakov (1963) 77,94–96,100
- Sorauf, J. E. 9
- sp.
  - *Aulopora* 99
  - *Catenipora* 76
  - *Favosites* 9,93
  - *Halysites* 9,11,70
  - *Heliolites* 11,13
  - *Lyellia* 11,13
  - *Palaeophyllum* **21**,9,10,12,13,17,18,25,34,*101*,*102*,**B**
  - *Paleofavosites* 93
  - *Pycnostylus?* 14
- sp?
  - *Columnaria* 13
  - *Cyathophyllum* 13
  - *Favosites* 13
  - *Lyellia?* 13
- sp. A
  - *Acidolites* **8**,11,17,18,*65*,**B**
  - *Aulopora* **20**,9,10,15,17–19,26,33,*40*,*97–99*,**B**
  - *Halysites* 74
  - *Halysites?* **12**,11,18,19,67,69,*73*,*74*,**B**
  - *Paleofavosites* **19**,14,15,18,41,46,79,87,89,*96*,97,**B**
  - *Plasmopora* 64
  - *Propora* **8**,11,18,19,45,47,*63*,**B**
  - *Protaraea* **8**,9,10,17,18,25,26,*66*,**B**
  - *Pycnostylus* **21**,14,16–18,20,33,*102*,*103*,**B**
  - *Rhabdotetradium* **20**,11,17,18,20,*99*,*100*,**B**
- sp. A of Bolton, *Propora* 52,54
- sp. indet.
  - favositid 14
  - halysitid 12
  - *Paleofavosites* 13,15,18
- sp. Type 2, *Acidolites* 65
- *Sparsisolenia* Stasinska 77,78
- *speciosa,*
  - *Lyellia* 59,60
  - *Propora* **6**,**7**,11,14,16–18,20,22,*38*,41,42,45,47,*58–62*,**B**
- *speciosa* (sp. aff.), *Propora* 58,60
- *speciosus, Heliolites* 58,60
- *spiroddensis, Palaeofavosites* 95
- Stanton *et al.* (1990) 19
- Stasinska (1967) 67,76–78,87,93,95,96
- State Route
  - 3 104
  - 79 105
  - D 105
  - W 104
- Stauriida Verrill 17,101
- Stauriidae Milne-Edwards and Haime 17,19,101
- Staurina Verrill 17,101
- Stearn (1956) 21,54,77,78,88,102,103
- Stearn (1989) 41
- Stechow (1922) 44,59,60
- Stel (1975) 77
- Stel and Oekentorp (1976) 78
- Stel and Oekentorp (1980) 78
- *Stelliporella parvistella* (Roemer) 32
- Stimpson (1858) 65
- Stonewall Formation 21,88,102
  - *t* marker bed 21
- Stony Mountain Formation 19,21,88
- *Streptelasma*
  - *leemonense* Elias 26,72,100
  - *subregulare* (Savage) 14,18,19
- *Stricklandia protriplesiana* (Amsden) 19
- Stumm (1965) 63
- *subelongus*
  - *Favosites* 11,13,55,78,86,87,89
  - *Paleofavosites* **13-17**,9–19,21,22,25,26,28–34,36,37, *38–40*,41,42,46,77,*78*,*79*,*81*,*82*,*84–89*,91,95,97,**B**
- *subelongus* (sp. cf.), *Paleofavosites* **17**,14,16,18,21,22,40,41,46,79,87,*89–91*,**B**
- *subregulare, Streptelasma* 14,18,19
- Sutton (1966) 43
- Swallow (1855) 13
- Sweden
  - Borenshult 61
  - Dalarna 54,61
  - Dalecarlia 54,61
  - Gotland 61,65,67,73,74,76,94
  - Kopparsvik 65
  - Korpklint 73
  - Öland 61
  - Östergotland 61
  - Ostrogothia 61
  - Treberga 61
- Sweet (1979) 21,45,88,102
- Sweet (1984) 21
- Sylvan Shale 9,10
- *syringoporoides,*
  - *Rhabdotetradium* 100
  - *Tetradium* 100

- Tabulata Milne-Edwards and Haime 8,17,18,40–42,44,66,**B**
- Tadzhikistan 45
- Taylor (1990) 25
- Tennessee 100
- Tentaculitidae Walcott 98
- Tesakov (1973) 34,39
- Tete des Morts Formation 105,**B**
- Tetradiida Okulitch 17,20,99
- Tetradiidae Nicholson 17,99
- *Tetradium* Dana 99
  - *cribriforme* (Etheridge) 100
  - *micropora* Bassler 100
  - *oklahomense* Bassler 100
  - *syringoporoides* Ulrich 99,100
- Texas 20,45,102
  - westernmost 19
- *thebensis, Lyellia* 13
- *thebesensis,*
  - *Lyellia* 9,11,13,45,52,55,58,65,89
  - *Plasmopora* 11,62
  - *Propora* **1-4**,9–14,16–20,22,25,28–34,*35*,36–38,41,42, *45–48*,*50–56*,58,62,64,85,**B**
- *thebesensis* (cf.), *Lyellia* 13

thebesensis (n. sp. aff.), *Propora* 58
thebesensis paucivesiculosa,
  Lyellia 45,52
  Propora 52
Thompson and Satterfield (1975) 8,18,19,104,105
Thompson, J. W. M. 9
Trenton
  Limestone 65
  Shales 99
trentonensis, *Aulopora* (?) 99
Tryplasma Lonsdale 21
Tryplasmatidae Etheridge 21
Tsagan-Del beds 17,61,62
Tubipora catenularia Linnaeus 67
tubulata,
  Porites 44
  Propora 55
tunicata (var.), *Propora conferta* 45,54
Twenhofel (1914) 77,88
Twenhofel (1916) 53,54,61
Twenhofel (1928) 45,53,59,60,76,77,88,98,102
Twenhofel, W. H. 98

U.K.
  Leinthall Earls 77
  Walsall 63
  Welsh Borderland 45,77
U.S. Route
  20 105
  52 105,106
  54 105
  61 105
  65 104
  77 104
U.S.A. 65
UI [University of Illinois at Urbana–Champaign, Urbana, Illinois, U.S.A.] 44,45,52,55,57–60,62–65,68,72–74,85–87,89, 92–94,117,118,120–123,126–130,133
United States **F**,20
  east-central **F**,7–9,14,17–22,28,38–41,43,45–47,51–54,56, 58,60–62,64,66,69,73,79,87,89,94,95,97,98,101,103,**B**
United States Geological Survey, Washington, D.C. 9,104
University of Illinois at Urbana–Champaign, Urbana, Illinois 9
University of Manitoba 9
University of New Orleans, New Orleans, Louisiana 9
University of North Carolina, Chapel Hill, North Carolina 9
Uralba Beds 70
Urals 21,95,96
USNM [National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.] 44,48,50–53,55–58,61–63,66,68,70–74,77,78,80–82, 84,89–92,94–97,99,100,102,104,116–136
Utah 88

Vauréal Formation 20,21,87,88,102
vaurealense, *Palaeophyllum* 102
venustus (cf.), *Favosites* 55
Veron and Pichon (1976) 42
Verrill (1865) 101
vetustus, *Porites* 65
Vik Formation 76
Visby beds 76
  Lower 76
  Upper 73,76
Volkova *et al.* (1978) 76,93
Vormsi Stage 61

Waddington, J. B. 9
walliensis, *Aulopora* 99
Way, H. G. 52
Webby (1975) 42,71
Webby (1977) 98,99
Webby and Semeniuk (1969) 42,70,71
Webby and Semeniuk (1971) 99,100
Webby *et al.* (1981) 70,99,100
Wedekind (1937) 77
Weller (1940) 104
Wenlock Shale 63
Weston, T. C. 62
White Head Formation 54,61
  Burmingham Member 88,93
White, R. D. 9,76
Whiteaves (1884) 102,103
Whitlow and Brown (1963) 20,106
Wilhelmi Formation 13–15,17–20,33,55,72,89,99,105,126,132,135,**B**
  Birds Member 15,105
  Schweizer Member 13,15,105
Willis and Ayre (1985) 31
Williston Basin 20,21
Willman (1962) 105
Willman (1973) 18,20,105,106
Winchell and Schuchert (1895) 99
Winder and Sanford (1972) 63,103
Witzke (1992) 63
Witzke and Kolata (1988) 20
Woolhope Limestone 44,45
Worsley *et al.* (1983) 76,93,95,96
Worthen (1866) 10
Wyoming 20,21,102

Yabe (1915) 73
yabei, *Propora* 45,54
Young (1988) 22
Young and Elias (1993) 35,38,39,41,43,45,78,82,83,94
Young and Noble (1989) 34
Young and Noble (1990a) 35,43
Young and Noble (1990b) 35,42,45,55,63,64,123
Young and Scrutton (1991) 24,27,28,30–32
Young *et al.* (1991) 43
Young, G. A. 9,44
Young, V. L. F. 9,44
YPM [Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A.] 44,98
Yü (1960) 76,102

Zeilstra, R. G. 9
zhejiangensis, *Catenipora* 76

BULLETINS OF AMERICAN PALEONTOLOGY
PALAEONTOGRAPHICA AMERICANA

Instructions for Authors

EDITORIAL POLICY

Bulletins of American Paleontology (begun in 1895) and *Palaeontographica Americana* (begun in 1916) are two of the oldest paleontological journals in the world. Since 1981 both series have shared the same large format (8½ × 11 inch pages, two columns per page, with 7 × 9 inch plates). *Bulletins of American Paleontology* publishes papers of approximately 50–200 printed pages and comprises two or more separate monographs in two volumes each year. *Palaeontographica Americana* publishes papers of 150 printed pages and larger and appears irregularly, usually every other year. [One printed page = approximately 3.6 double-spaced typed manuscript pages; an approximate minimum size for manuscripts suitable for either monograph series is 100–125 manuscript pages.] Shorter manuscripts are not normally considered for publication in either series, as numerous other journals are available for such papers. Authors with manuscripts of 25–50 printed pages are encouraged, however, to contact the editor to discuss potential options.

Bulletins of American Paleontology and *Palaeontographica Americana* are publication outlets for significant longer paleontological monographs for which high quality photographic illustrations and the large quarto format are required. Although the focus of both series is on contributions that use fossils as their primary database, submissions are also welcome that include substantial neontological data that can be applied to paleontological problems. Contributions on any taxon are welcome, including macroinvertebrates, vertebrates, plants, and protists. Although most contributions focus on systematics, it is expected that the systematic treatment presented will be placed in biostratigraphic, biogeographic, paleoenvironmental, paleoecological and/or evolutionary context.

Each manuscript is reviewed by at least two reviewers and the Editor. Authors are encouraged to suggest potential reviewers for their manuscripts. Reviews are not anonymous and the names of reviewers are published inside the front cover of each issue.

FORMAT REQUIREMENTS

Text Usage

Authors are referred to *The Chicago Manual of Style* (fourteenth edition; University of Chicago Press, 1993) for general guidelines on usage. Where there is conflict, current style in *Bulletins* and *Palaeontographica* prevails.

All manuscripts must be in English. Authors of manuscripts containing extensive discussion of material from non-English speaking countries are encouraged to prepare an additional abstract in the appropriate non-English language.

Double-space the entire manuscript, including abstract, text, references, tables, figure captions, and appendices. Number all pages, beginning with the title page and including tables, table captions, figures, figure captions, plates and plate captions. Do not justify the right margin. When using computerized word processors, italicized words may either be underlined or italicized, but use only one or the other throughout the manuscript.

All manuscripts should contain a table of contents, lists of text-figures and/or tables, and a short, informative abstract that includes names of all new taxa. Acknowledgements should follow the INTRODUCTION in the text.

All measurements should be given in the metric system, alone or in addition to their English system equivalents.

Four hierarchical levels of section headings are used:

1) centered, all upper-case
2) centered, Upper- and lower-case
3) centered italics
4) Flush left, italics, indented.

For example:

INTRODUCTION

Study Area

Geological Setting

Surficial Stratigraphy.- - -

Spell out the words "Plate", "Text-figure", and "Table" in running text; abbreviate them to "Pl." and "Text-fig." (but keep "Table") in parenthetical expressions. Such terms should have initial caps when referring to illustrations in your own manuscript but should be lower case throughout when referring to illustrations in other literature.

Spell out "new genus", "new species" in headings in text and "Explanations of Plates", but abbreviate to "n. sp.", "n. gen." in running text, tables, and text-figures.

Use "*et al.*" in text-citation of papers with three or more authors.

Spell out generic names at the beginning of a sentence and when used with "sp." Generic and subgeneric names may be abbreviated after being given in full within a paragraph and if there is no chance of confusion with other generic names.

Use all authors' names for taxa (e.g., *Xus yus* Jones and Smith; *Xus yus* Jones in Smith; *Xus yus* Jones, Smith and Wallace). In text discussion, use full author name and date for a taxon only when there is danger of ambiguity or lack of clarity. Include taxonomic references in the References Cited when such references are unlikely to be familiar or widely known. The Editor reserves the right to delete or request that the author(s) add such information.

Capitalize formally proposed and accepted time and time-rock designations (*e.g.*, Middle Eocene, Late Miocene); do not capitalize informal designations (*e.g.*, middle Pliocene, late Mesozoic, early Maastrichtian).

Add diacritical marks, as appropriate, to non-English words.

Italicize commonly used non-English words and abbreviations, such as *incertae sedis, e.g., i.e., non, pro, sensu, aff., cf.*, and *et al.* Do not italicize "cf." when it is used with italicized generic and specifc names.

Cite informal references with author, type of communication, year year (*e.g.*, "Wilson, written commun., 1985", or "Jones, oral commun., 1984").

Use past tense for published or other previous work in the text; (*e.g.*, "Conrad (1830) noted that. . .").

References cited in the text should be cited in chronological order; references published in the same year should be cited alphabetically.

Spell out whole numbers zero through nine; write numbers 10 and above in Arabic numerals. Exceptions: spell out all numbers beginning a sentence, and treat alike all similar numbers in connected groups or in the same sentence; do not use numerals for some and spell out others. Use Arabic numerals for all measurements.

Use personal pronouns if you wish, but make certain their number is correct. Don't use "we" to describe the single author of a manuscript.

Use hyphens as "-"; *en*-dashes [separating end members of ranges of dates, measurements, pages, etc.] as "- -"; *em*-dashes [significant pauses in sentences; blank spaces in tables, indicating "no observation" and following the period in side headings (*e.g.*, "Table 1.- - - ")] as "- - -".

SYSTEMATIC PALEONTOLOGY

All manuscripts must include a section called "Introduction to Systematic Paleontology", which, in turn, should include, but is not limited to:

"Philosophical Considerations" (What is a fossil species of the group you are describing? How does this differ from an equivalent-level taxonomic entity of a related living organism, whatever that may be? What is your personal taxonomic philosophy?) In contributions including significant consideration of phylogenetic reconstruction, appropriate attention must be given to details of method (*e.g.*, approach taken, assumptions made, computer program or algorithm used, character codings and their justification).

"Format" (style and scope of synonymy used; a guide to the ensuing discussion, including terms such as *non, pro, sensu, aff., cf.*, or other qualifiers, localities, formations, etc.)

"Terminology, Measurement, and Abbreviation" used.

"Acronyms and Locations of Specimen Repositories".

A full summary of systematics up to at least the class level must be given at least once, including authors and dates for all taxa. Taxa left in "open nomenclature" should be in the format discussed by Bengston, P., 1988, *Palaeontology*, vol. 31, p. 223–227.

Headings in "Systematic Paleontology" section should be as follows (note capitalization and bolding):

Phylum **BRACHIOPODA** Dumeril, 1806

Order **ORTHIDA**
Schuchert and Cooper, 1932

Family **DALMANELLIDAE**
Schuchert, 1913

Genus **LEVENEA**
Schuchert and Cooper, 1931

Type species.- - -*Orthis subcarinata* Hall, 1857, p. 43.

Levenea subcarinata (Hall, 1857)

Synonymies should be in "short form"; *i.e.*, complete with respect to citations listed, but not including the article, book, or periodical titles in each citation, only author, date, page, plate, and figure. All references so cited must be included in the REFERENCES CITED. The following format should be used:

Pentagonia unisulcata (Conrad, 1841)

Plate 6, figures 7- -13

Atrypa unisulcata Conrad, 1841, p. 56.

Atrypa uniangulata Hall, 1861, p. 101.
Meristella? unisulcata (Conrad). Hall, 1862, p.158, pl. 2, figs. 17, 20--23 (not figs. 19, 24, 25).
Non *Meristella unisulcata* (Conrad). Nettleroth, 1889, p. 99, pl. 15, figs. 9--16.
Pentagonia unisulcata (Conrad). Stauffer, 1915, p. 104, 245 (not pp. 160, 171, 175, 234); Goldring, 1935, p. 148, figs. 53B--D.

Section headings within systematic descriptions should be consistent for all lower taxa discussed. All such headings should be flush left, indented, italicized, upper- and lower-case, and followed by a period and em-dash. For example:

Description.---
Diagnosis.---
Types.---
Other material examined.---
Occurrence.---
Discussion.---

When citing types, spell out the kind of type, and use repository acronym and catalogue number. Give repository and catalogue number for figured, measured, and mentioned specimens (such specimens are hypotypes, even if they are not figured, and must be susceptible to relocation by future investigators). Specify the repository prefix acronym for all sample and locality numbers.

REFERENCES CITED

Spell out bibliographic details in their entirety, including periodical titles. Entries not in Roman alphabet may be presented in their original type or characters, but must also include at least a Roman alphabet translitteration, and preferably an English translation of at least the title.

Follow these formats for citations in the REFERENCES CITED:

Article in journal:

Adegoke, O. S.

1967. *Wyattella*, a new turritellid genus from the Eocene of Colombia, South America. Journal of Paleontology, vol. 41, pp. 1095--1100.

An author's name is not repeated in successive citations:

Gardner, J. A.

1931. Relation of certain foreign faunas to Midway fauna of Texas. American Association of Petroleum Geologists Bulletin, vol. 15, pp. 149--160.

1935. The Midway group of Texas. University of Texas Bulletin 3301, 403 pp., 28 pl.

Article in edited volume:

Bretsky, S. S.

1979. Recognition of ancestor-descendant relationships in invertebrate paleontology. *in* Phylogenetic analysis and paleontology. J. Cracraft and N. Eldredge, *eds.*, Columbia University Press, New York, pp. 113--164.

Article in press:

Emslie, S. D.

1994. An early Irvingtonian avifauna from Leisey Shell Pit, Florida. Bulletin of the Florida Museum of Natural History (in press).

Book, single author:

Beerbower, J.

1968. Search for the past. An introduction to paleontology. 2nd edition. Prentice-Hall, Englewood Cliffs, NJ, 512 pp.

Book, multiple authors:

Fretter, V., and Graham, A.

1962. British prosobranch molluscs. Ray Society, London, 755 pp.

Dissertation or thesis:

Allison, R. C.

1967. The Cenozoic stratigraphy of Chiapas, Mexico, with discussion of the classification of the Turritellidae and selected Mexican representatives. unpublished PhD thesis, University of California, Berkeley, 450 pp.

Paper presented at meeting:

Allmon, W. D.

1987. Multiple modes of homeomorphy in Cenozoic turritellid gastropods and their evolutionary implications. Geological

Society of America, Abstracts with Programs, vol. 19, no. 7, p. 570.

Treatise on Invertebrate Paleontology

Cox, L.

1960. General characteristics of Gastropoda. *in* Treatise on invertebrate paleontology. R. C. Moore, *ed*., Part I, Mollusca 1, by J. B.Knight *et al*., Geological Society of America and University of Kansas Press, pp. I84--I169.

Field guides:

Beauchamp, R. G.

1984. Stratigraphy and depositional environments of the Brightseat and Aquia Formations, Maryland and Virginia. *in* Cretaceous and Tertiary stratigraphy, paleontology and structure, southwestern Maryland and northeastern Virginia. American Association of Stratigraphic Palynologists Field Trip Guidebook. N. O. Fredericksen and K. Kraft, *eds*., pp. 78--111.

INDEX

Each issue of both *Bulletins of American Paleontology* and *Palaeontographica Americana* includes an index. Construction of the index is the responsibility of the author(s) and is requested at page proof stage.

ILLUSTRATIONS AND TABLES

High-quality illustrations have been a hallmark of both *Bulletins of American Paleontology* and *Palaeontographica Americana* since their inception and are expected of all manuscripts.

TEXT FIGURES

Prepare text-figures for reproduction as single column (82 mm; 3¼ inches) or two column (178 mm; 7 inches) width. All text-figures should be prepared so as to be read with the journal in normal reading position (*i.e.*, if illustrations must be more than 7″ wide, consider putting them on two facing pages; if 14″ is not wide enough, consider recasting the illustration as a foldout.

All text-figures should be submitted one to a page as either glossy prints or high-quality photocopies, at publication size.

Prepare text-figure captions one to a page.

A foldout may be particularly helpful for stratigraphic range data, *e.g.*, taxa arising in stratigraphic order if there is a clear trend, or, if such a trend is not present, alphabetically by genus, and within that by species. In this way, individual taxa can be much more easily located, and their "bedmates" more comfortably comprehended. Such charts can be published as foldouts. Foldouts must be drafted to be no more than 9″ high, but they may be up to 25″ wide. These are inserted inside the front or back covers, and nothing is printed on the first fold, so that the foldout can be viewed while reading the monograph, without having to flip back and forth.

PLATES

Photographic plates should be prepared with great care, with special attention given to contrast within individual images as well as composition of the plate as a whole. Plates may be prepared on either black or white backgrounds. Each image on a plate should be designated by an Arabic numeral. Empty space among images should be minimized. Maximum dimensions of plates are 178 mm × 229 mm (7 inches × 9 inches). Original plate photomounts should have oversize cardboard backing and strong tracing paper overlays.

Prepare an "Explanation" of each plate on a separate sheet including a taxonomic designation, repository, specimen number, locality, and magnification for each specimen illustrated.

The initial manuscript submission should include at least one set of glossy prints. The review copies may include high-quality photocopies. Original plate photomounts should be retained by the author until the manuscript has been accepted for publication.

TABLES

Tables should be prepared one to a page. Table captions should be prepared separately, one to a page. Avoid vertical lines in Tables. Use abbreviations in tables as little as possible, and define, in the INTRODUCTION TO SYSTEMATIC PALEONTOLOGY (see above) any you must use that might be ambiguous.

AUTHOR CHARGES

Authors are required to defray a portion of the costs of publication. These costs are assessed not as page charges, but rather on the basis of illustrations. Currently, the following cost schedule is in effect:

Photographic plates, 7″ × 9″	$120.00
Text-figures	$35.00
Foldouts (each)	$100.00

Authors should expect to pay $2.00 per line for alterations to copy at or after page proof stage. Authors must be PRI members at time of publication. Annual membership is $25.

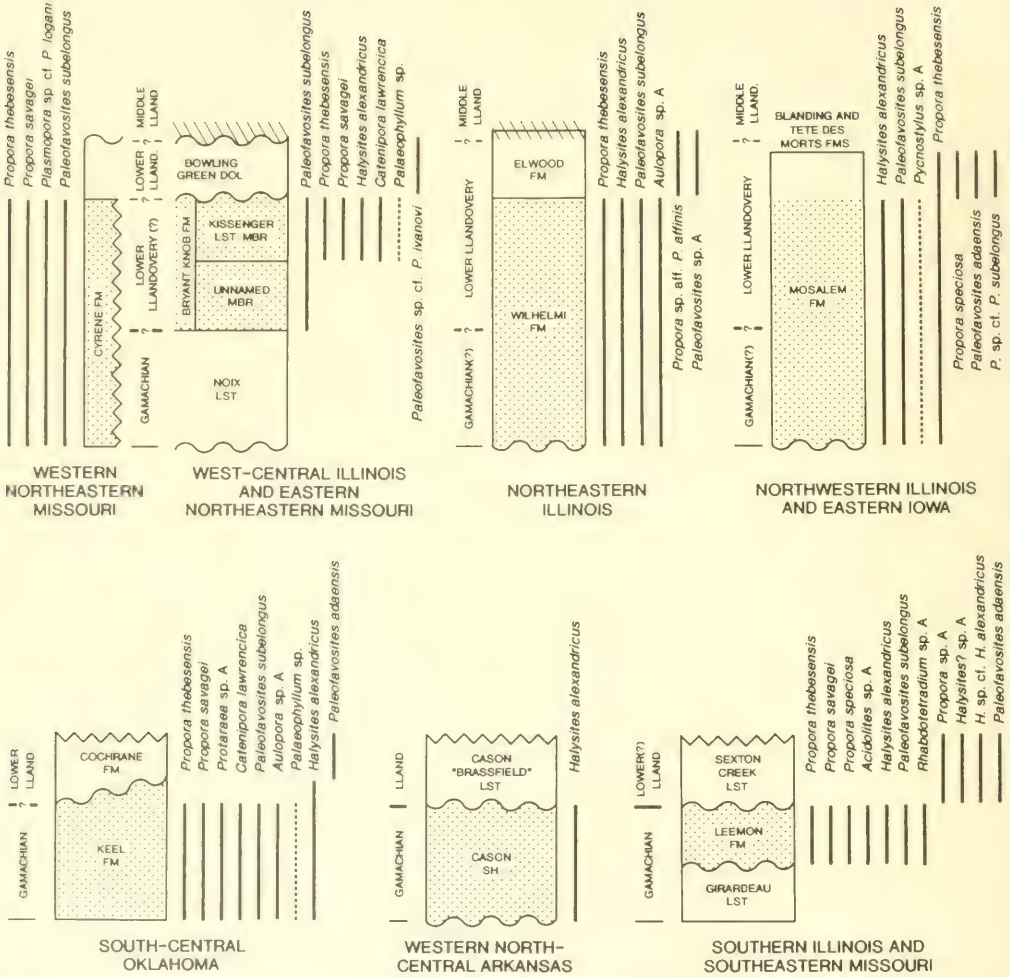
SUBMISSION PROCEDURE

Submit three paper copies of the manuscript, including figures, plates and tables. After the review process is completed, authors are encouraged to submit revised manuscripts on disk.

Turnaround time from acceptance to publication runs from as little as nine months to as much as two years, depending on the size and original condition of the manuscript, as well as the number of manuscripts currently in the publication queue.

Authors receive 10 free reprints of their paper. Additional copies can be purchased at 40% off the list price.

Address submissions and questions regarding publication to: Editor, Paleontological Research Institution, 1259 Trumansburg Road, Ithaca, NY 14850, Telephone: (607) 273-6623, FAX: (607) 273-6620, email (inquiries only): wda1@cornell.edu.


WESTERN NORTHEASTERN MISSOURI
Propora thebesensis
Propora savagei
Plasmopora sp. cf. P. logani
Paleofavosites subelongus
CYRENE FM
GAMACHIAN
LOWER LLANDOVERY (?)
LOWER LLAND.
MIDDLE LLAND
WEST-CENTRAL ILLINOIS AND EASTERN NORTHEASTERN MISSOURI
BOWLING GREEN DOL
BRYANT KNOB FM
KISSENGER LST MBR
UNNAMED MBR
NOIX LST
Paleofavosites subelongus
Propora thebesensis
Propora savagei
Halysites alexandricus
Catenipora lawrencica
Palaeophyllum sp.
Paleofavosites sp. cf. P. ivanovi
NORTHEASTERN ILLINOIS
ELWOOD FM
WILHELMI FM
GAMACHIAN(?)
LOWER LLANDOVERY
MIDDLE LLAND
Propora thebesensis
Halysites alexandricus
Paleofavosites subelongus
Aulopora sp. A
Propora sp. aff. P. affinis
Paleofavosites sp. A
NORTHWESTERN ILLINOIS AND EASTERN IOWA
BLANDING AND TETE DES MORTS FMS
MOSALEM FM
GAMACHIAN(?)
LOWER LLANDOVERY
MIDDLE LLAND.
Halysites alexandricus
Paleofavosites subelongus
Pycnostylus sp. A
Propora thebesensis
Propora speciosa
Paleofavosites adaensis
P. sp. cf. P. subelongus
SOUTH-CENTRAL OKLAHOMA
COCHRANE FM
KEEL FM
GAMACHIAN
LOWER LLAND
Propora thebesensis
Propora savagei
Protaraea sp. A
Catenipora lawrencica
Paleofavosites subelongus
Aulopora sp. A
Palaeophyllum sp.
Halysites alexandricus
Paleofavosites adaensis
WESTERN NORTH-CENTRAL ARKANSAS
CASON "BRASSFIELD" LST
CASON SH
GAMACHIAN
LLAND
Halysites alexandricus
SOUTHERN ILLINOIS AND SOUTHEASTERN MISSOURI
SEXTON CREEK LST
LEEMON FM
GIRARDEAU LST
GAMACHIAN
LOWER(?) LLAND
Propora thebesensis
Propora savagei
Propora speciosa
Acidolites sp. A
Halysites alexandricus
Paleofavosites subelongus
Rhabdotetradium sp. A
Propora sp. A
Halysites? sp. A
H. sp. cf. H. alexandricus
Paleofavosites adaensis

Text-figure 8.—Composite stratigraphic sections showing uppermost Ordovician (Gamachian) and lowermost Silurian (Llandovery) units and distribution of colonial corals in the east-central United States (see Text-fig. 1A, foldout inside front cover). Thicknesses of units are not to scale. Range lines of species (solid for Tabulata, dotted for Rugosa) indicate presence within, but not necessarily throughout, the intervals indicated (for details, see Text-figs. 2–7 and text). Strata containing colonial corals of the Edgewood Assemblage are stippled; colonial corals in overlying strata represent the Silurian assemblage. Hachures indicate the *Platymerella manniensis* zone.

PREPARATION OF MANUSCRIPTS

Bulletins of American Paleontology usually comprises two or more separate papers in two volumes each year. The series is a publication outlet for significant, longer paleontological monographs (*i.e.*, more than approximately 50 printed pages), for which high quality photographic illustrations and the large quarto format are required.

Submissions are welcome from any author, regardless of institutional or organizational affiliation. Authors must, however, be members of the Paleontological Research Institution at time of publication; annual membership is currently US$25.00. Publication costs of the *Bulletins* are heavily subsidized by the Institution, but authors are currently required to pay illustration charges at a rate of $120.00 per plate and $35.00 per text-figure.

Important references for style and format are 1) *Bulletins of American Paleontology* "Instructions for Authors" (volume 108, number 347, pages 149–153); 2) *Chicago Manual of Style* (fourteenth edition) 1993. Recent issues of the *Bulletins* provide useful guides but note changes with the "Instructions for Authors" mentioned above.

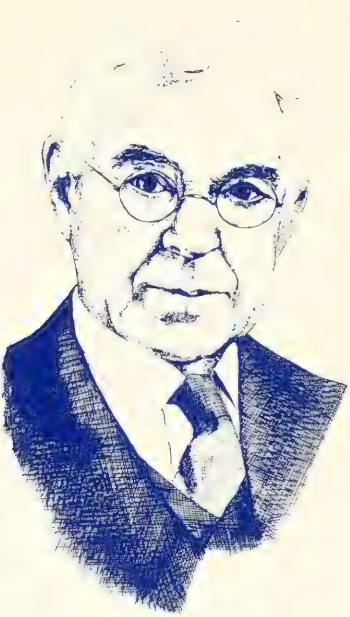
Manuscripts must be typewritten, and double-spaced *throughout* (including direct quotations, tables and references). All manuscripts should contain a table of contents, lists of text-figures and/or tables, and a short, informative abstract that includes names of all new taxa. Format should follow that of recent numbers in the series. All measurements must be given in the metric system, alone or in addition to their English system equivalents. The maximum dimensions for photographic plates are 178 mm × 229 mm (7 inches × 9 inches; outlined on this page). Single-page text-figures should be drafted for reproduction as single column (82 mm; 3¼ inches) or full page (178 mm; 7 inches) width, but arrangements can be made to publish text-figures that must be larger.

Authors must provide three (3) printed copies of the text and accompanying illustrative material. Authors are *strongly* encouraged to prepare their manuscripts on word processors, as this considerably expedites publication. On initial submission, however, only printed copies of the manuscript should be sent; the disk copy should be retained so that revisions can be made after the review process. The text and line-drawings may be reproduced xerographically, but glossy prints at publication size must be supplied for all half-tone illustrations and photographic plates. These prints should be identified clearly on the back.

Referenced publication titles *must be spelled out in their entirety.* Particular care should be given to reference format. Consult the "Instructions for Authors," referred to above, as several changes have been introduced with that issue. Citations of illustrations within the text bear initial capitals (*e.g.*, Plate, Text-figure), but citations of illustrations in other works appear in lower-case letters (*e.g.*, plate, text-figure).

Format of systematic descriptions should follow that in any recent number of the *Bulletins.*

Original plate photomounts should have oversize cardboard backing and strong tracing paper overlays. These photomounts should be retained by the author until the manuscript has been formally accepted for publication. The approximate position of each text-figure in the text should be indicated. Explanations of plates and text-figures should follow the References Cited.



Gilbert Dennison Harris
(1864 - 1952)

Founder of the *Bulletins of American Paleontology* (1895)

ISBN 0-87710-434-6

QE
701
B8X
NH

Bulletins of American Paleontology

Begun in 1895

VOLUME 108, NUMBER 348 **MARCH 5, 1996**

Pliensbachian (Lower Jurassic) Ammonites of the Queen Charlotte Islands, British Columbia

by

Paul L. Smith
and
Howard W. Tipper

Paleontological Research Institution
1259 Trumansburg Road
Ithaca, New York, 14850 U.S.A.

Celebrating 100 years
1895–1995

PALEONTOLOGICAL RESEARCH INSTITUTION

Officers

PRESIDENT . . . . JOHN C. STEINMETZ
VICE-PRESIDENT . . . . RICHARD E. PETIT
SECRETARY . . . . HENRY W. THEISEN
TREASURER . . . . PAMELA WAIT
DIRECTOR . . . . WARREN D. ALLMON

Trustees

R. TUCKER ABBOTT (to 6/30/96)
BRUCE M. BELL (to 6/30/96)
CARLTON E. BRETT (to 6/30/98)
WILLIAM L. CREPET (to 6/30/97)
J. THOMAS DUTRO, JR. (to 6/30/96)
SHIRLEY K. EGAN (to 6/30/98)
ANTON J. EGNER (to 6/30/97)
M. G. HARASEWYCH (to 6/30/98)
HARRY G. LEE (to 6/30/97)
AMY R. MCCUNE (to 6/30/97)
SAMUEL T. PEES (to 6/30/98)
RICHARD E. PETIT (to 6/30/96)
EDWARD B. PICOU (to 6/30/98)
GARY ROSENBERG (to 6/30/96)
CONSTANCE M. SOJA (to 6/30/97)
JAMES E. SORAUF (to 6/30/97)
JOHN C. STEINMETZ (to 6/30/97)
SUSAN B. STEPHENS (to 6/30/96)
HENRY W. THEISEN (to 6/30/98)
MARY KANE TROCHIM (to 6/30/98)
PAMELA WAIT (to 6/30/96)
THOMAS C. WHITELEY (to 6/30/97)

Trustees Emeritus

HARRY A. LEFFINGWELL
ROBERT M. LINSLEY
RAYMOND VAN HOUTTE
WILLIAM P. S. VENTRESS

BULLETINS OF AMERICAN PALEONTOLOGY
and
PALAEONTOGRAPHICA AMERICANA

WARREN D. ALLMON . . . . EDITOR

Reviewers for this issue

RUSSELL L. HALL
AXEL VON HILLEBRANDT

A list of titles in both series, and available numbers and volumes may be had on request. Volumes 1–23 of *Bulletins of American Paleontology* are available from Periodicals Service Company, 11 Main St., Germantown, New York 12526 USA. Volume 1 of *Palaeontographica Americana* has been reprinted by Johnson Reprint Corporation, 111 Fifth Ave., New York, NY 10003 USA.

Subscriptions to *Bulletins of American Paleontology* may be started at any time, by volume or year. Current price is US $62.50 per volume. Numbers of *Palaeontographica Americana* are priced individually, and are invoiced separately on request.

for additional information, write or call:

Paleontological Research Institution
1259 Trumansburg Road
Ithaca, NY 14850 USA
(607) 273-6623
FAX (607) 273-6620

⊘ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

Bulletins of American Paleontology

Begun in 1895

VOLUME 108, NUMBER 348 MARCH 5, 1996

SMITHSONIAN
MAR 29 1996
LIBRARIES

Pliensbachian (Lower Jurassic) Ammonites of the Queen Charlotte Islands, British Columbia

by

Paul L. Smith
and
Howard W. Tipper

Paleontological Research Institution
1259 Trumansburg Road
Ithaca, New York, 14850 U.S.A.

ISSN 0007-5779
ISBN 0-87710-439-5
Library of Congress Catalog Card Number: 95-71053

Printed in the United States of America
Allen Press, Inc.
Lawrence, KS 66044 U.S.A.

CONTENTS

	Page
Abstract	7
Introduction	7
Acknowledgments	8
Lithostratigraphy	8
The Sandilands Formation	9
The Ghost Creek Formation	11
The Fannin Formation	11
Regional Setting and Correlations	11
Biostratigraphy	13
Systematic Paleontology	16
Introduction	16
Terminology and Abbreviations	18
Systematics	18
Phylloceratidae	18
Phylloceras	18
Juraphyllitidae	20
Tragophylloceras	20
Cymbitidae	23
Cymbites	23
Oxynoticeratidae	24
Fanninoceras (*Fanninoceras*)	27
Fanninoceras (*Charlotticeras*)	32
Gleviceras?	33
Polymorphitidae	33
Gemmellaroceras	33
Polymorphites	35
Acanthopleuroceras	35
Tropidoceras	37
Phricodoceratidae	40
Phricodoceras	40
Eoderoceratidae	41
Pseudoskirroceras	41
Miltoceras	42
Dubariceras	42
Metaderoceras	43
Dactylioceratidae	46
Reynesoceras	46
Reynesocoeloceras	49
Amaltheidae	51
Amaltheus	51
Liparoceratidae	52
Liparoceras (*Becheiceras*)	52
Oistoceras	53
Hildoceratidae	54
Arieticeras	56
Leptaleoceras	57
Fontanelliceras	58
Canavaria?	59
Oregonites?	59
Fieldingiceras	60
Fuciniceras	61
Protogrammoceras (*Protogrammoceras*)	63
Protogrammoceras (*Matteiceras*)	67
Genus indet.	67
Lioceratoides (*Lioceratoides*)	68
Lioceratoides (*Pacificeras*)	71
Tiltoniceras	72
Appendix: Locality Register	73
References cited	77
Plates	85
Index	116

LIST OF ILLUSTRATIONS

Text-figure Page

1. The Queen Charlotte Islands, British Columbia, and the location of measured sections A through C 8
2. The central Queen Charlotte Islands showing the location of measured sections A through E 9
3. South-central Graham Island with the location of measured sections F and G; borehole H; and isolated localities I01 through I17 10
4. The lithostratigraphic units of the Maude and upper Kunga groups 11
5. Standard Pliensbachian zones of North America utilized in this study and approximate correlation with primary standard zonation of northwestern Europe 11
6. Legend for the stratigraphic columns and faunal charts of Text-figures 7 to 14, and 16 to 24 12
7. Lithostratigraphy and fossil localities of section A, southeastern Kunga Island 13
8. Lithostratigraphy and fossil localities of section B, northern Louise Island 13
9. Lithostratigraphy and fossil localities of section C, north shore of Cumshewa Inlet 14
10. Lithostratigraphy and fossil localities of section D, Whiteaves Bay 14
11. Lithostratigraphy and fossil localities of section E, Fannin Bay, southeast Maude Island 15
12. Lithostratigraphy and fossil localities of section F, the Forest Service Road 19 Quarry 15
13. Lithostratigraphy and fossil localities of section G, Rennell Junction 16
14. Lithostratigraphy and fossil localities of Well Core H 16
15. Correlation of Pliensbachian units in the Queen Charlotte Islands 17
16. The ammonite fauna and biostratigraphy of section A 18
17. The ammonite fauna and biostratigraphy of section B 19
18. The ammonite fauna and biostratigraphy of section C 19
19. The ammonite fauna and biostratigraphy of section D 19
20. The ammonite fauna and biostratigraphy of section E fold-out inside back cover
21. The ammonite fauna and biostratigraphy of section F 20
22. The ammonite fauna and biostratigraphy of section G 21
23. The ammonite fauna and biostratigraphy of well core H 21
24. The ammonite fauna found at isolated localities on southern Graham Island 22
25. Whorl shape cross-sections for species of the Phylloceratidae and Cymbitidae 23
26. Traces of the septal suture for species of the Phylloceratidae, Cymbitidae, Polymorphitidae and Dactylioceratidae 24
27. A specimen of *Fanninoceras* (*Fanninoceras*) *fannini* broken open to show the inner whorls 25
28. The ontogeny of whorl shape in *Fanninoceras* (*F.*) *fannini*, the type species of *Fanninoceras* (*Fanninoceras*) showing the characteristic change from depressed inner to compressed outer whorls 26
29. Typical combinations of volution and ornamentation for species of *Fanninoceras* at shell diameters greater than 20 mm 27
30. Whorl shape cross-sections for species of *Fanninoceras* 29
31. Traces of the septal suture for species of *Fanninoceras* 30
32. Whorl shape cross-sections for species of the Polymorphitidae 37
33. Whorl shape cross-sections for species of the Eoderoceratidae 44
34. Traces of the septal suture for species of the Eoderoceratidae 45
35. Whorl shape cross-sections for species of the Dactylioceratidae 48
36. Whorl shape cross-sections for species of the Amaltheidae and Liparoceratidae 52
37. Whorl shape cross-sections for species of the Arieticeratinae 55
38. Traces of the septal suture for species of the Hildoceratidae 62
39. Whorl shape cross-sections for species of the Harpoceratinae 65

LIST OF TABLES

Table Page

1. Measurements of *Phylloceras bonarellii* Bettoni, 1900 23
2. Measurements of *Phylloceras* sp. 23
3. Measurements of *Tragophylloceras* new species? 23
4. Measurements of *Cymbites centriglobus* (Oppel, 1862) 24
5. Measurements of *Cymbites laevigatus* (J. de C. Sowerby, 1827) 26
6. Measurements of *Fanninoceras* (*Fanninoceras*) *bodegae* McLearn, 1932 27
7. Measurements of *Fanninoceras* (*Fanninoceras*) *carlottense* McLearn, 1930 28
8. Measurements of *Fanninoceras* (*Fanninoceras*) *crassum* McLearn, 1932 29
9. Measurements of *Fanninoceras* (Fanninoceras) *fannini* McLearn, 1930 30
10. Measurements of *Fanninoceras* (*Fanninoceras*) *kunae* McLearn, 1930 31
11. Measurements of *Fanninoceras* (*Fanninoceras*) *latum* McLearn, 1930 31
12. Measurements of *Fanninoceras* (*Fanninoceras*) sp. 2 32
13. Measurements of *Fanninoceras* (*Charlotticeras*) *carteri,* new species 32
14. Measurements of *Fanninoceras* (*Charlotticeras*) *maudense,* new species 33
15. Measurements of *Gemmellaroceras aenigmaticum* (Gemmellaro, 1884) 34
16. Measurements of *Polymorphites confusus* (Quenstedt, 1856) 35
17. Measurements of *Acanthopleuroceras thomsoni,* new species 36
18. Measurements of *Tropidoceras actaeon* (d'Orbigny, 1844) 38
19. Measurements of *Tropidoceras flandrini flandrini* (Dumortier, 1869) 38
20. Measurements of *Tropidoceras masseanum rotunda* (Futterer, 1893) 39
21. Measurements of *Tropidceras* aff. *rursicosta* (Buckman, 1918) 39
22. Measurements of *Reynescoceras colubriforme* (Bettoni, 1900) 47
23. Measurements of *Reynesoceras ragazzonii* (Hauer, 1861) 48
24. Measurements of *Reynesocoeloceras grahami,* new species 50
25. Measurements of *Reynesocoeloceras mortilleti* (Meneghini, 1875) 50
26. Measurements of *Amaltheus stokesi* (Sowerby, 1818) 51
27. Measurements of *Amaltheus viligaensis* (Tuchkov, 1954) 51
28. Measurements of *Liparoceras* (*Becheiceras*) *bechei* (J. Sowerby, 1821) 53
29. Measurements of *Oistoceras compressum,* new species 54
30. Measurements of *Arieticeras disputabile* (Fucini, 1908) 55
31. Measurements of *Arieticeras lupheri* Imlay, 1968 56
32. Measurements of *Arieticeras* cf. *ruthenense* (Reynès, 1868) 56
33. Measurements of *Leptaleoceras* aff. *accuratum* (Fucini, 1931) 57
34. Measurements of *Leptaleoceras compressum* (Monestier, 1934) 57
35. Measurements of *Leptaleoceras* sp. 58
36. Measurements of *Fontanelliceras* sp. 59
37. Measurements of *Oregonites*? *dawsoni,* new species 59
38. Measurements of *Fieldingiceras fieldingii* (Reynès, 1868) 61
39. Measurements of *Fieldingiceras pseudofieldingii* (Fucini, 1904) 61
40. Measurements of *Protogrammoceras* (*Protogrammoceras*) *aequiondulatum* (Bettoni, 1900) 64
41. Measurements of *Protogrammoceras* (*Protogrammoceras*) sp. 64
42. Measurements of *Protogrammoceras* (*Protogrammoceras*) *kurrianum* (Oppel, 1862) 66
43. Measurements of *Protogrammoceras* (*Protogrammoceras*) *skidegatense,* new species 66
44. Measurements of *Lioceratoides* (*Lioceratoides*) *allifordense* (McLearn, 1930) 68
45. Measurements of *Lioceratoides* (*Lioceratoides*) *involutum,* new species 69
46. Measurements of *Lioceratoides* (*Lioceratoides*) *maurelli* (McLearn, 1930) 69
47. Measurements of *Lioceratoides* (*Lioceratoides*) sp. juv. 70
48. Measurements of *Lioceratoides* (*Pacificeras*) *angionus* (Fucini, 1931) 71
49. Measurements of *Lioceratoides* (*Pacificeras*) *propinquum* (Whiteaves, 1884) 72
50. Measurements of *Tiltoniceras antiquum* (Wright, 1882) 73

PLIENSBACHIAN (LOWER JURASSIC) AMMONITES OF THE QUEEN CHARLOTTE ISLANDS, BRITISH COLUMBIA

Paul L. Smith and Howard W. Tipper

Department of Geological Sciences, University of British Columbia,
6339 Stores Road, Vancouver, British Columbia, V6T 1Z4 CANADA
Sedimentary and Cordilleran Geoscience Branch,
Geological Survey of Canada, 100 West Pender Street
Vancouver, British Columbia, V6B 1R8 CANADA

ABSTRACT

The lower Maude and upper Kunga groups in the central Queen Charlotte Islands provide the most complete and fossiliferous Pliensbachian sequences in North America. Outcrops on Maude Island and at Whiteaves Bay serve as either type or reference sections for the Imlayi, Whiteavesi, Freboldi, Kunae and Carlottense zones of the standard North American zonation.

The Sandilands Formation of the Kunga Group is mostly pre-Pliensbachian in age but exposures on Kunga Island are as young as Whiteavesi Zone. The Sandilands Formation and the succeeding Ghost Creek Formation of the Maude Group were deposited in fairly deep, euxinic waters subjected to diminishing pyroclastic and volcaniclastic input, the latter by turbidity currents. Shallowing culminated in the deposition of the coarser sediments of the Fannin Formation which were laid down in higher energy, well oxygenated waters. Most of the Ghost Creek Formation is assignable to the Imlayi Zone with its upper 10 m or so as young as the Whiteavesi Zone; at one level in the Whiteavesi Bay section, it is as young as the Freboldi Zone. The Fannin Formation ranges in age from the Whiteavesi to the Carlottense zones and locally into the Toarcian.

This report is the first comprehensive, stratigraphically controlled study of the Pliensbachian ammonoids of the Queen Charlotte Islands. Seven hundred and fourteen localities have yielded at least 1600 specimens assignable to approximately 85 species representing 32 genera or sub-genera and 11 families of ammonoids. *Charlotticeras* is established as a new subgenus of *Fanninoceras* and *Pacificeras* (Repin, 1970) is recognized as a subgenus of *Lioceratoides*. The following new species are established (in alphabetical order): *Acanthopleuroceras thomsoni, Fanninoceras (Charlotticeras) carteri, F. (C.) maudense, Lioceratoides (Lioceratoides) involutum, Oistoceras compressum, Oregonites? dawsoni, Protogrammoceras (Protogrammoceras) skidegatense,* and *Reynesocoeloceras grahami.*

INTRODUCTION

The Queen Charlotte Islands, known to the native people as Haida Gwaii, form a 280 km long archipelago off the central coast of British Columbia, Canada (Text-fig. 1). The Islands are part of the Wrangell tectonostratigraphic terrane which constitutes the greater part of the Insular Belt, the region west of the Coast Plutonic Complex.

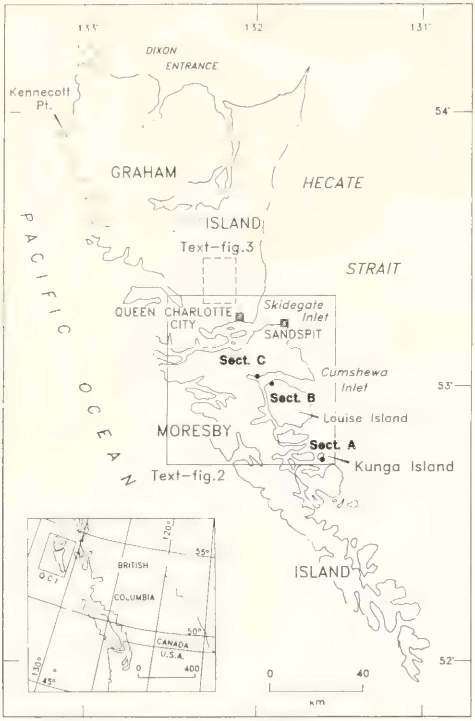
Richardson (1873) published the first geological account of the Queen Charlotte Islands but it was not until the work of Sutherland Brown (1968) that a detailed geological map was produced. A comprehensive study of the Jurassic stratigraphy published by Cameron and Tipper (1985) was followed in 1987 by a three-year multidisciplinary project under the auspices of the Geological Survey of Canada's Frontier Geoscience Program addressing the hydrocarbon potential of the Queen Charlotte basin (Woodsworth, 1991). An important focus of this multidisciplinary study, of which this report is a component, was the Lower Jurassic part of the stratigraphic column whose thermally mature, organic-rich shales form potential hydrocarbon source rocks (Vellutini and Bustin, 1991a, 1991b).

The only existing paleontological reports on the Queen Charlotte Islands containing illustrations of Pliensbachian ammonites are those of Whiteaves (1884), McLearn (1932), Frebold (1970), and Smith *et al.* (1988). Whiteaves and McLearn did not recognize the Pliensbachian age of their fossils; Frebold's report lacked stratigraphic information and, as with Smith *et al.*'s regional study, it was less than comprehensive with respect to the Queen Charlotte Islands. The need to rectify this lack of detailed biostratigraphic and systematic information concerning the Pliensbachian ammonites of the Queen Charlotte Islands can be justified on four grounds:

(i) There is no other place in North America that offers such relatively continuous stratigraphic sequences yielding well preserved and often abundant ammonites. The Queen Charlotte Islands will serve as the type area for much of the North American Lower Jurassic ammonite zonation (Smith *et al.*, 1988, 1994; Jakobs *et al.*, 1994a, 1994b; Pálfy *et al.*, 1994) and will therefore be central to precise correlations between

---

Geological Survey of Canada Contribution Number 41493



Text-figure 1.—The Queen Charlotte Islands, British Columbia, and the location of measured sections A through C.

the allochthonous terranes, as well as between the terranes and the craton.

(ii) The Queen Charlotte Islands will also be the center of a web of circum-Pacific and ultimately global correlations because of their unique biogeographic setting where Tethyan, east Pacific and scattered Boreal forms may be found in the same beds. Pliensbachian ammonite biogeography has already been used to constrain the Early Jurassic position of Wrangellia and details of ammonite paleontology are essential in assessing the relative importance of the Hispanic Corridor as a biogeographic link between the western Tethys and Pacific oceans during the Early Jurassic (Smith and Tipper, 1986; Smith, 1988; Smith and Westermann, 1990).

(iii) Lower Jurassic sequences in the Queen Charlotte Islands are yielding microfossils as well as ammonites (Carter *et al.*, 1988; Bown, 1991; Tipper *et al.*, 1991; Smith *et al.*, 1994). This offers opportunities (a) to calibrate macrofossil and microfossil zonations providing more accurate and precise correlations over a broader range of geological and sampling conditions, and (b) indirectly to correlate microfossil sequences with the northwest European standard zonation.

(iv) Because of the hydrocarbon potential of the Queen Charlotte Islands, accurate correlation of the lithostratigraphic units is important as an aid to understanding the geological and sedimentological history of the region. The fossil illustrations will also be of use to those engaged in producing more detailed geological maps.

ACKNOWLEDGMENTS

We thank the many geologists and paleontologists of the Geological Survey of Canada and the Frontier Geoscience Program who collected material and shared their stratigraphic information with us. Of particular importance have been Bruce Cameron, formerly of the Geological Survey of Canada, and Beth Carter, Giselle Jakobs, and Jozsef Pálfy, all former graduate students at the University of British Columbia.

The following helped at various times in the laboratory and in preparing the manuscript: Joanna Beyers, Myles Gao, David Handel, and Robin Manley. Photography was by Kate Gordanier-Smith, drafting by Tonia Williams, and Bev Vanlier typed the manuscript. Sincere thanks are extended to all these people.

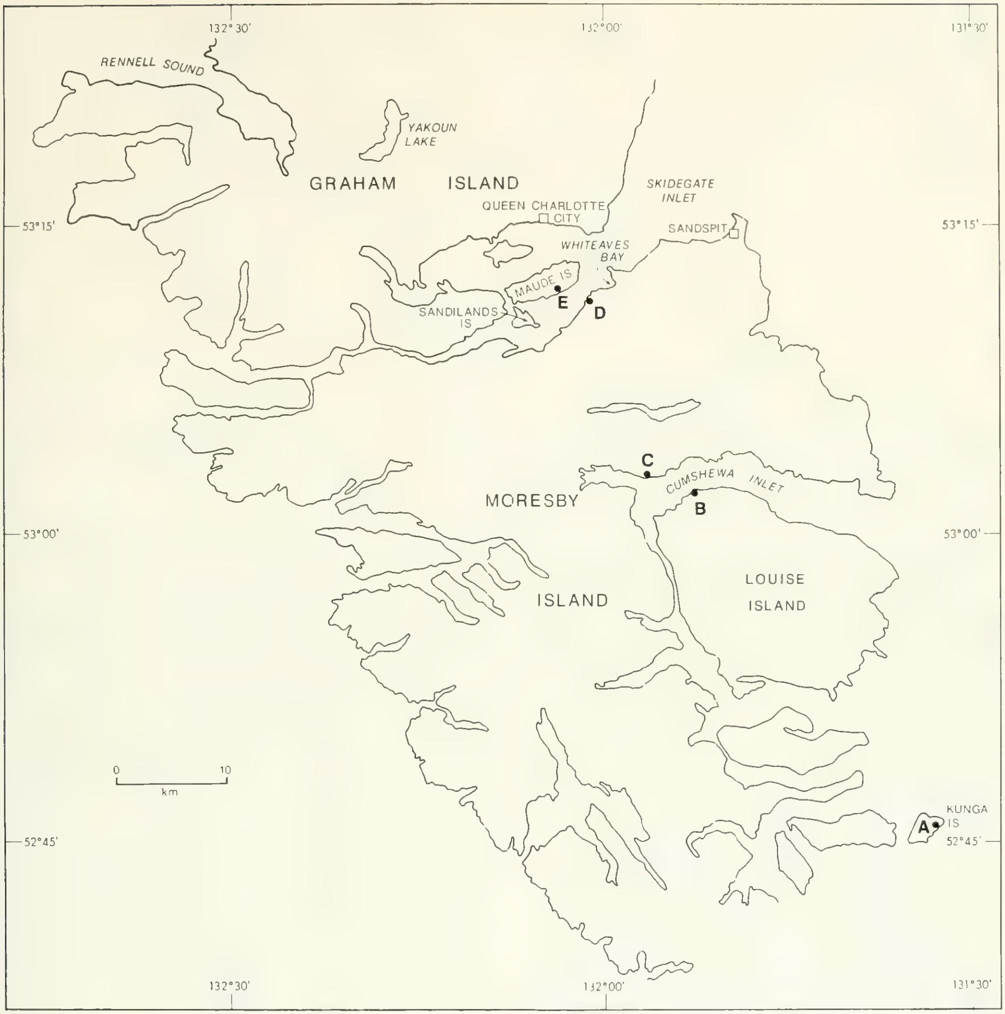
Over the years we have had valuable discussions with the following ammonite paleontologists: John Callomon and Desmond Donovan (University College, London); Jean-Louis Dommergues and Christian Meister (University of Dijon); Michael Howarth (British Museum); Axel von Hillebrandt (Technische Universität, Berlin); and René Mouterde (Facultés Catholiques, Lyon).

The manuscript benefitted from the critical comments and helpful suggestions of Warren Allmon (Paleontological Research Institution), Jim Haggart (Geological Survey of Canada), Russell Hall (University of Calgary), and Axel von Hillebrandt.

LITHOSTRATIGRAPHY

The Pliensbachian rocks of the heavily forested Queen Charlotte Islands crop out from Kunga Island in the southeast, across Louise and Moresby Islands to southern Graham Island in the northwest, a distance of approximately 90 km (Text-figs. 2 and 3). Shorelines and streams offer the best exposures but on southern Graham Island logging road cuts and road-metal quarries have increased rock exposure and improved accessibility.

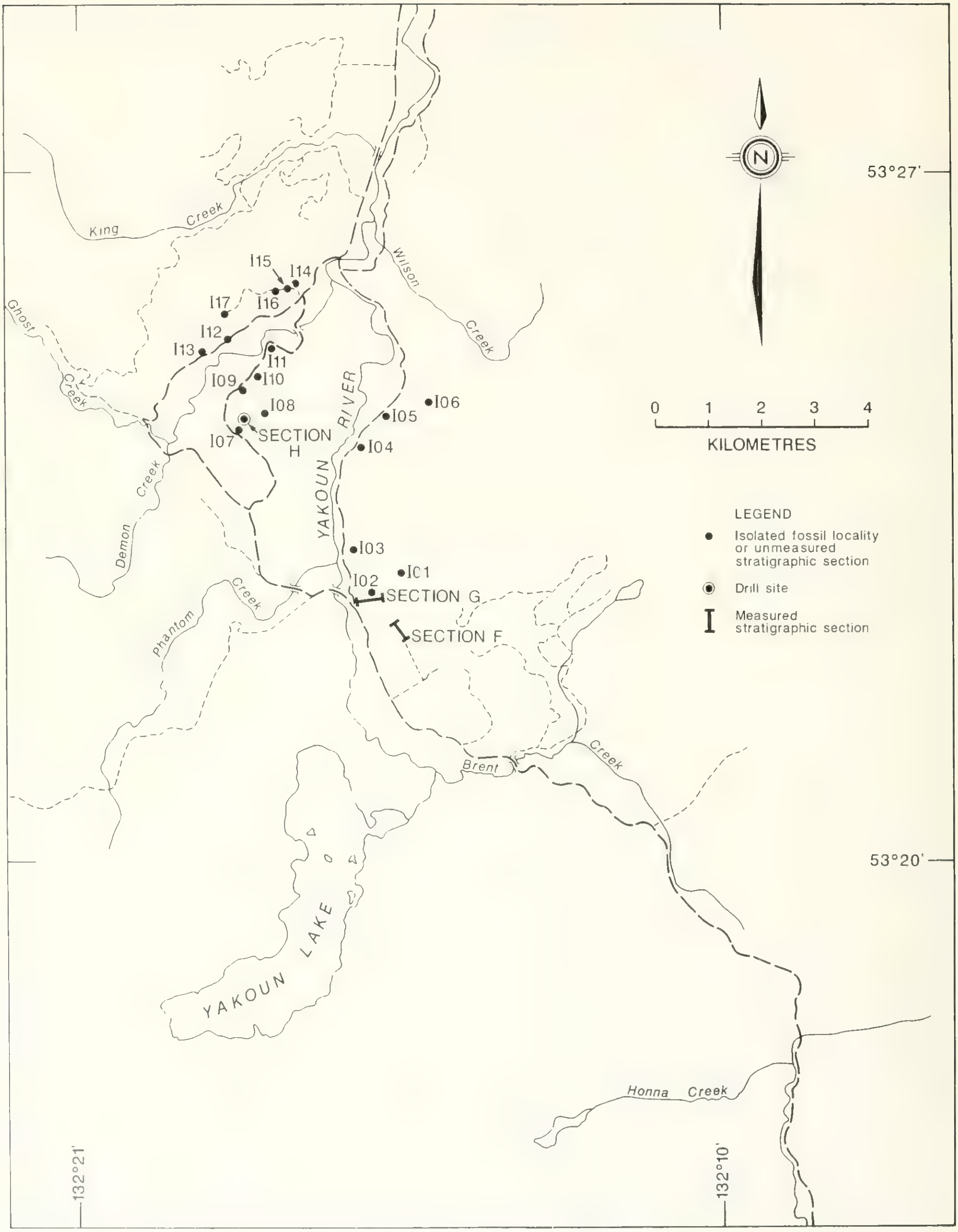
Pliensbachian ammonites have been collected from the Kunga and Maude groups (Text-fig. 4) which together range in age from the Carnian to the Aalenian.

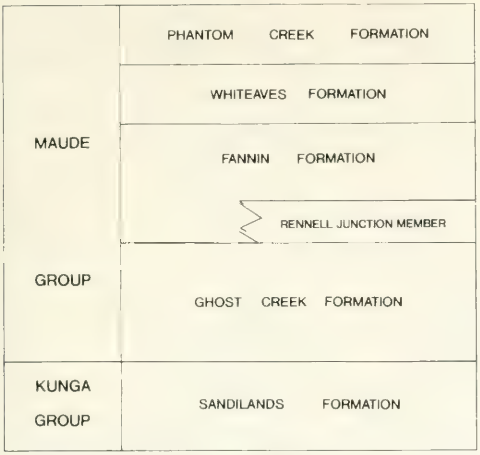

132°30'
132°00'
131°30'
RENNELL SOUND
YAKOUN LAKE
GRAHAM ISLAND
QUEEN CHARLOTTE CITY
SKIDEGATE INLET
SANDSPIT
53°15'
WHITEAVES BAY
MAUDE IS
E
D
SANDILANDS IS
C
CUMSHEWA INLET
B
MORESBY
53°00'
ISLAND
LOUISE ISLAND
0
10
km
KUNGA IS
A
52°45'
132°30'
132°00'
131°30'

Text-figure 2.—The central Queen Charlotte Islands showing the location of measured sections A through E. See Text-figure 1.

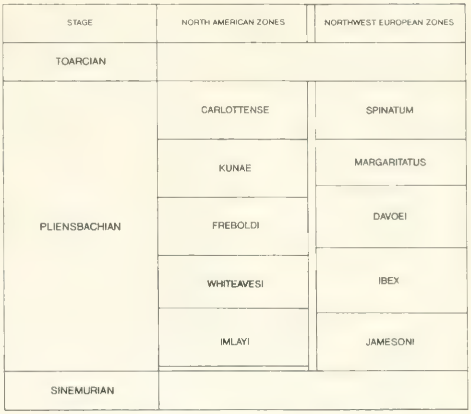
As a result of early Middle Jurassic contractional deformation, the Maude Group is missing in some areas and the Bajocian Yakoun Group rests with marked angular unconformity on Sinemurian parts of the Kunga Group (Lewis and Ross, 1991; Thompson *et al.*, 1991). The formations of interest are the Sandilands, Ghost Creek, and Fannin formations as defined by Cameron and Tipper (1985) to which the reader should refer to supplement the brief descriptions of lithology and depositional setting given below.

The Sandilands Formation consists of several hundred meters of thinly bedded dark grey to black siltstone interbedded with graded, lithic sandstones and grey to white tuffs; volcanic breccia is present locally but bioturbation is conspicuous by its absence. Most of the unit is Sinemurian in age (Pálfy *et al.*, 1990;


53°27'
53°20'
132°21'
132°10'
N
0 1 2 3 4
KILOMETRES
LEGEND
● Isolated fossil locality or unmeasured stratigraphic section
◉ Drill site
I Measured stratigraphic section
King Creek
Wilson Creek
Ghost Creek
Demon Creek
Phantom Creek
Brent Creek
Honna Creek
YAKOUN RIVER
YAKOUN LAKE
I01
I02
I03
I04
I05
I06
I07
I08
I09
I10
I11
I12
I13
I14
I15
I16
I17
SECTION H
SECTION G
SECTION F



Text-figure 4.—The lithostratigraphic units of the Maude and upper Kunga groups.



STAGE	NORTH AMERICAN ZONES	NORTHWEST EUROPEAN ZONES
TOARCIAN		
PLIENSBACHIAN	CARLOTTENSE	SPINATUM
	KUNAE	MARGARITATUS
	FREBOLDI	DAVOEI
	WHITEAVESI	IBEX
	IMLAYI	JAMESONI
SINEMURIAN		

Text-figure 5.—Standard Pliensbachian zones of North America utilized in this study and approximate correlation with the primary standard zonation of northwestern Europe.

Pálfy *et al.,* 1994) but the boundary between the Sandilands and Ghost Creek formations is diachronous, such that outcrops of the Sandilands in the southern part of the islands are as young as Early Pliensbachian (Pálfy *et al.*, 1990; Smith *et al.*, 1990; Tipper *et al.*, 1991). The tuff and graded lithic sandstone beds are also thicker to the south, suggesting that the Sandilands Formation was deposited in a quiet, fairly deep-water, possibly euxinic setting that was periodically subject to deposition of air-fall tuff and turbidites whose source was to the south or southwest.

The Ghost Creek Formation is a recessive unit reaching a thickness in excess of 60 m. It contrasts markedly with the underlying Sandilands Formation in having more shale and only rare ash or tuffaceous beds. The shales are dark and pyritic. Occasional sandstones and nodular limestones are present and the top of the formation becomes locally glauconitic in the north. Oil stains and bitumen are pervasive. Benthic fossils and bioturbation are not common but are more frequent in the upper part of the unit generally and throughout the unit in more southerly exposures.

The Ghost Creek Formation was deposited in fairly deep water that shallowed and perhaps became less euxinic both to the south and upsection. The setting appears to be similar to that of the Sandilands Formation except that volcanic activity had waned leading to only minor pyroclastic and coarse volcaniclastic input.

The Fannin Formation is a coarsening upward sequence that rests conformably on the Ghost Creek Formation. The transitional beds were initially named the Rennell Junction Formation by Cameron and Tipper (1985) but as the unit proved to be unmappable, it was included within a redefined Fannin Formation by Tipper *et al.* (1991) and is here referred to as the Rennell Junction Member.

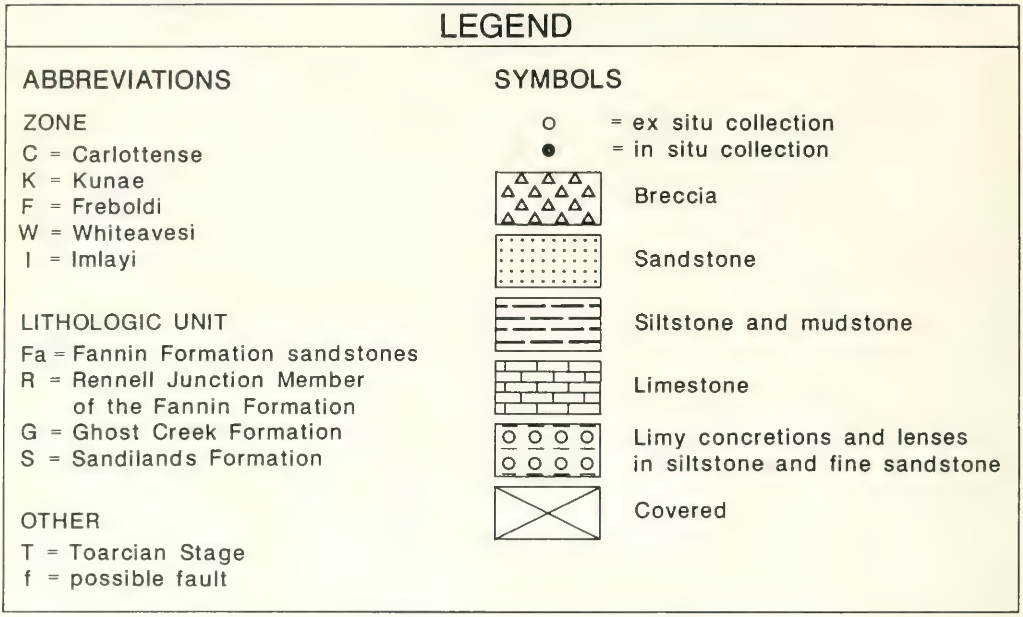
The Rennell Junction Member typically ranges in thickness from 15 to 40 m but may locally reach a thickness of up to 75 m. It consists of fine grained sandstone, siltstone, and shale with irregular limestone beds and nodules. The upper part of the Fannin Formation consists of coarser, more resistant, and thicker bedded sandstones compared with the Rennell Junction Member. This interval is fairly heterogeneous, however, and concretionary limestones, tuffs, breccias, and conglomerate lenses are locally developed. Chamosite ooliths can be abundant in the uppermost part of the unit where trace fossils, sparsely present throughout, become slightly more common.

REGIONAL SETTING AND CORRELATIONS

Zones indicated on measured sections are the North American Pliensbachian ammonite zones described by

←

Text-figure 3.—South-central Graham Island with the location of measured sections F and G; borehole H; and isolated localities I01 through I17. See Text-figure 1.


LEGEND
ABBREVIATIONS
ZONE
C = Carlottense
K = Kunae
F = Freboldi
W = Whiteavesi
I = Imlayi
LITHOLOGIC UNIT
Fa = Fannin Formation sandstones
R = Rennell Junction Member of the Fannin Formation
G = Ghost Creek Formation
S = Sandilands Formation
OTHER
T = Toarcian Stage
f = possible fault
SYMBOLS
○ = ex situ collection
● = in situ collection
Breccia
Sandstone
Siltstone and mudstone
Limestone
Limy concretions and lenses in siltstone and fine sandstone
Covered

Text-figure 6.—Legend for the stratigraphic columns and faunal charts of Text-figures 7 to 14, and 16 to 24.

Smith *et al.* (1988). These zones and their approximate European correlatives are illustrated in Text-figure 5.

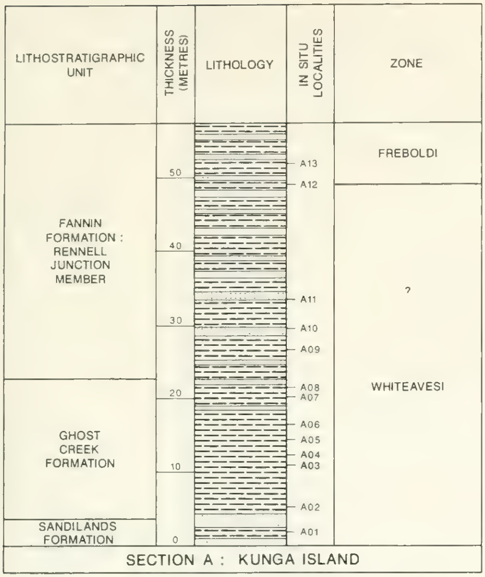
Details of lithology and lithostratigraphy for measured sections A through G and well core H are illustrated in Text-figures 6 through 14 which also show the zones present and the stratigraphic position of each fossil locality. Regional correlations are summarized in Text-figure 15.

As previously mentioned, limited exposures on Kunga Island demonstrate that a small portion of the Sandilands Formation is Pliensbachian in age. The unit is therefore at least partly coeval with the Ghost Creek and Fannin Formations. The bulk of the Ghost Creek Formation is Imlayi Zone in age but at most localities the upper part is as young as Whiteavesi Zone.

The transition from the Ghost Creek to the Fannin Formation occurs within the Whiteavesi Zone at most localities where control is good; the exception is in Whiteaves Bay (section D) where it occurs in the lowest Freboldi Zone. The transition from the Rennell Junction Member to the coarser sandstones of the upper Fannin Formation occurs near the boundary between the Freboldi and Kunae zones, usually within the Freboldi Zone. Although there is variation in the thickness of individual zones, there are no persistent lateral trends that might point to the relative proximity of sediment sources. Taken together, these observations argue for fairly uniform conditions across the sampled area during the deposition of the Ghost Creek and Fannin formations; perhaps the sections are arranged along depositional strike.

The lithologic, stratigraphic, trace fossil, and micropaleontological evidence suggests that the Pliensbachian part of the stratigraphic sequence represents a regressive event (Cameron and Tipper, 1985). The lower Ghost Creek and Sandilands formations accumulated in a stable back-arc setting in fairly deep, predominantly euxinic waters. Evidence for shallowing begins in the upper Ghost Creek Formation and culminates in the uppermost Fannin Formation where sediments were laid down in higher energy, well oxygenated waters. As has been noticed elsewhere in the world and, incidentally, in rocks of similar age, chamosite ironstones and sediments rich in chamosite ooliths characteristically occur near the top of regressive sequences. They formed in shallow seas near low lying, well vegetated land in a warm humid climate (Hallam and Bradshaw, 1979).

In summary: (i) the top of the Sandilands Formation is locally as young as the Whiteavesi Zone; (ii) the bulk


LITHOSTRATIGRAPHIC UNIT
THICKNESS (METRES)
LITHOLOGY
IN SITU LOCALITIES
ZONE
FANNIN FORMATION : RENNELL JUNCTION MEMBER
GHOST CREEK FORMATION
SANDILANDS FORMATION
0
10
20
30
40
50
A01
A02
A03
A04
A05
A06
A07
A08
A09
A10
A11
A12
A13
FREBOLDI
?
WHITEAVESI
SECTION A : KUNGA ISLAND

Text-figure 7.—Lithostratigraphy and fossil localities of section A, southeastern Kunga Island. See Text-figure 6 for legend and Text-figure 16 for the fauna present.

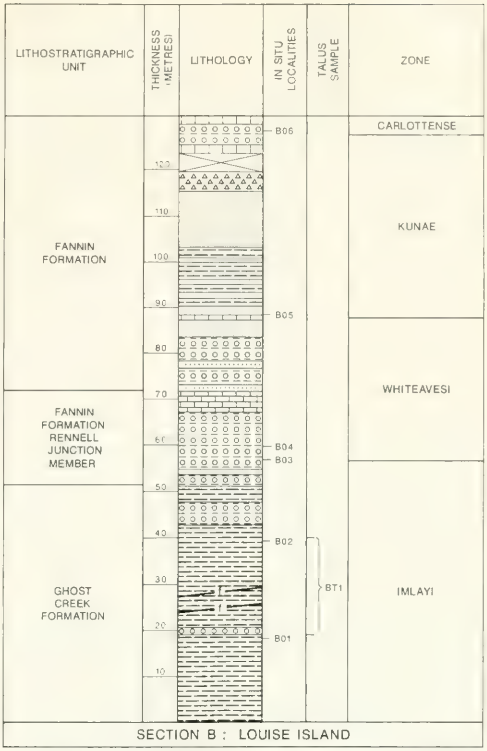
of the Ghost Creek Formation is assignable to the Imlayi Zone, its upper 10 m or so assignable to the Whiteavesi Zone and at one level in the Whiteaves Bay section it is as young as the Freboldi Zone; (iii) the Rennell Junction Member of the Fannin Formation predominantly ranges in age from the Whiteavesi to the Freboldi Zone; (iv) the sandstones of the upper Fannin Formation range in age from the Freboldi to the Carlottense Zone.

BIOSTRATIGRAPHY

Our approach to zonations and the naming of zones is as follows (Callomon, 1984; Smith *et al.*, 1988; Thomson and Smith, 1992; Jakobs *et al.*, 1994):

(i) No zonation can be worldwide in extent and some zonations may be restricted to a particular facies. For regionally extensive, biogeographically distinct areas, however, a standard zonation may be erected for a given group of organisms.

(ii) Standard zones are recognized on the basis of co-occurrences of species that are distinct from superjacent and subjacent assemblages. These stratigraphically distinct co-occurrences maintain their superpositional relationships throughout the geographic area in question.

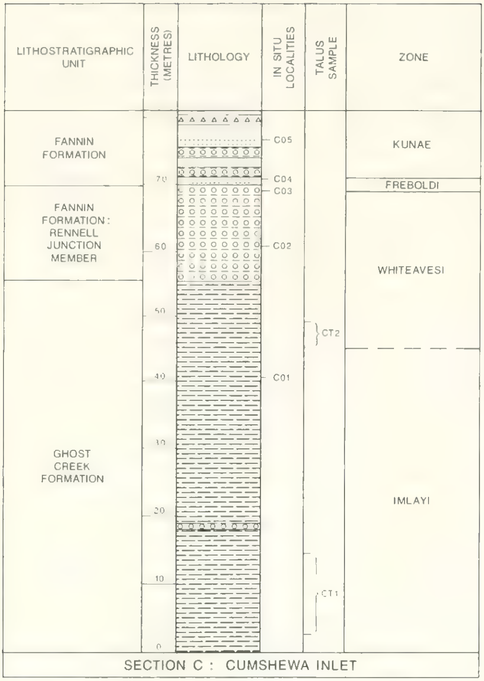

LITHOSTRATIGRAPHIC UNIT
THICKNESS (METRES)
LITHOLOGY
IN SITU LOCALITIES
TALUS SAMPLE
ZONE
FANNIN FORMATION
FANNIN FORMATION RENNELL JUNCTION MEMBER
GHOST CREEK FORMATION
10
20
30
40
50
60
70
80
90
100
110
120
B01
B02
B03
B04
B05
B06
BT1
CARLOTTENSE
KUNAE
WHITEAVESI
IMLAYI
SECTION B : LOUISE ISLAND

Text-figure 8.—Lithostratigraphy and fossil localities of section B, northern Louise Island. See Test-figure 6 for legend and Text-figure 17 for the fauna present. Base of section is faulted.

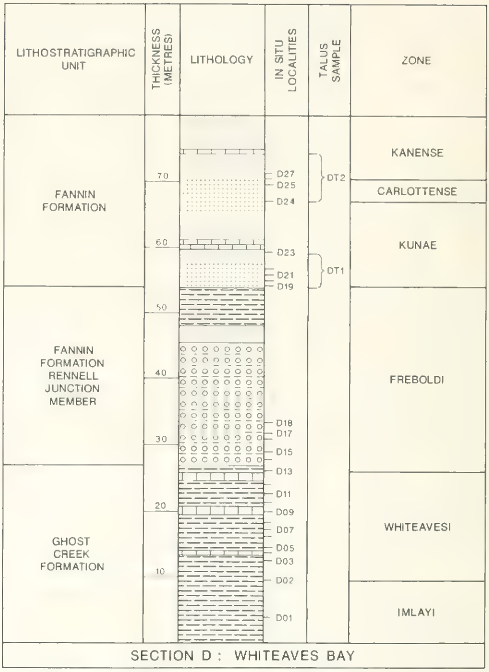
(iii) Standard zones are characterized by type sections, where the superpositional relationships are most clearly demonstrated and where zonal boundaries may be drawn. The base of a zone automatically defines the top of the subjacent zone.

(iv) By convention, standard ammonite zones are named using the non-italicized, capitalized trivial name of a species that is characteristic of that zone although not necessarily restricted to it. It is, of course, not necessary to collect the zonal ammonite to demonstrate the presence of the zone. The typography of standard zones distinguishes them from the full, italicized names of less formal zones, *e.g.*, provisional assemblages, zones used for local correlation, single taxa ranges.

(v) One standard zonation is selected as the primary standard to which all secondary standards are correlated with as much precision as possible. In the case


LITHOSTRATIGRAPHIC UNIT
THICKNESS (METRES)
LITHOLOGY
IN SITU LOCALITIES
TALUS SAMPLE
ZONE
FANNIN FORMATION
FANNIN FORMATION: RENNELL JUNCTION MEMBER
GHOST CREEK FORMATION
70
60
50
40
30
20
10
0
C05
C04
C03
C02
C01
CT2
CT1
KUNAE
FREBOLDI
WHITEAVESI
IMLAYI
SECTION C : CUMSHEWA INLET

Text-figure 9.—Lithostratigraphy and fossil localities of section C, north shore of Cumshewa Inlet. See Text-figure 6 for legend and Text-figure 18 for the fauna present. Base of section is faulted.

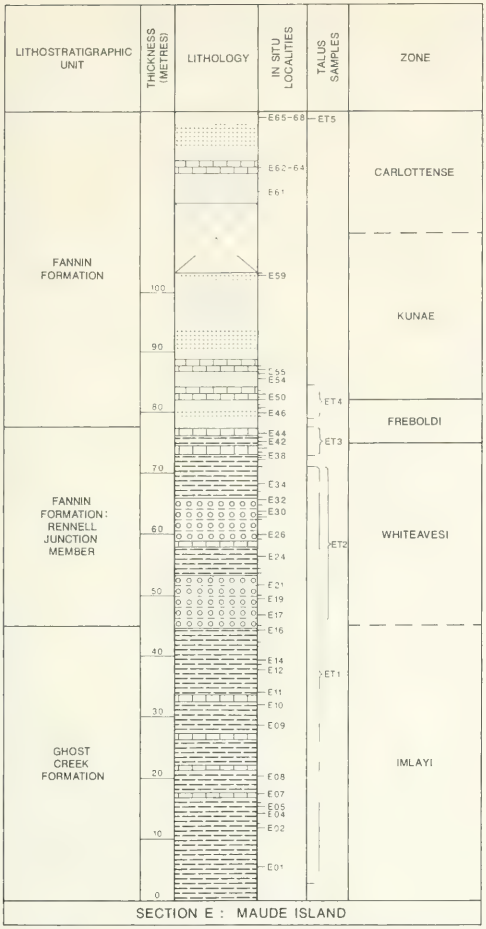

LITHOSTRATIGRAPHIC UNIT
THICKNESS (METRES)
LITHOLOGY
IN SITU LOCALITIES
TALUS SAMPLE
ZONE
FANNIN FORMATION
FANNIN FORMATION RENNELL JUNCTION MEMBER
GHOST CREEK FORMATION
70
60
50
40
30
20
10
D27
D25
D24
DT2
D23
D21
D19
DT1
D18
D17
D15
D13
D11
D09
D07
D05
D03
D02
D01
KANENSE
CARLOTTENSE
KUNAE
FREBOLDI
WHITEAVESI
IMLAYI
SECTION D : WHITEAVES BAY

Text-figure 10.—Lithostratigraphy and fossil localities of section D, Whiteaves Bay. See Text-figure 6 for legend and Text-figure 19 for the fauna present.

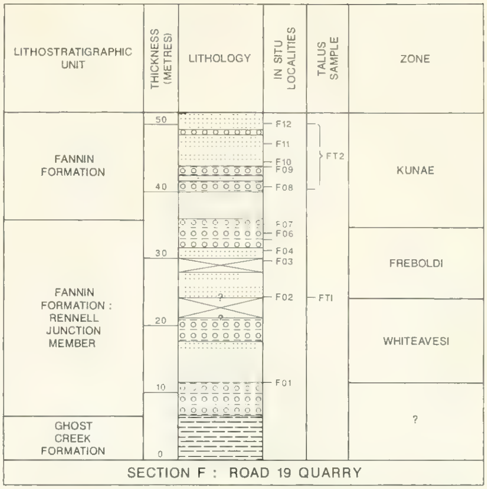
of the Lower Jurassic ammonites discussed in this report, the Northwest European zonation (Dean *et al.*, 1961) is the primary standard and the North American zonation (Smith *et al.*, 1988) is the secondary standard (Text-fig. 5).

The collections on which this report is based were made by the authors and numerous other geologists over the course of many years. The collecting began at the end of the last century and in some cases the same locality has been visited several times by different geologists. To bring some order to this situation we have, where possible, assigned the localities to a standardized labelling system where the letter prefix indicates, from south to north, the measured stratigraphic section and the number indicates, in ascending order, the stratigraphic position of the locality as illustrated in Text-figures 6 to 14. Where specimens were not in place or where there was uncertainty as to stratigraphic position in the case of old collections, the section letter prefix is followed by the letter 'T' denoting talus. We have shown in Text-figures 6 to 13 the approximate stratigraphic interval from which these collections originated. A complete listing of the standardized locality numbers and the original locality numbers is given in the Appendix together with the precise geographic position of the measured stratigraphic sections (A through G), the drilling site (H), and isolated fossil localities (I). Text-figures 16 through 24 indicate the ammonite fauna at each locality and the North American ammonite zones present.

The relationship of the Imlayi Zone to underlying faunal assemblages is the subject of continuing research. It appears that the *Tetraspidoceras* assemblage of Pálfy *et al.* (in press) spans the Sinemurian-Pliensbachian boundary and consequently the base of the Imlayi Zone does not correspond to the base of the Pliensbachian. The Imlayi Zone is the thickest of the Pliensbachian zones recognized in the Queen Charlotte Islands but its fauna is amongst the least diverse. *Pseudoskirroceras* and *Miltoceras* are restricted to the zone whereas species of *Tropidoceras*, that are more characteristic of the upper part of the zone, range upwards


LITHOSTRATIGRAPHIC UNIT
THICKNESS (METRES)
LITHOLOGY
IN SITU LOCALITIES
TALUS SAMPLES
ZONE
FANNIN FORMATION
FANNIN FORMATION: RENNELL JUNCTION MEMBER
GHOST CREEK FORMATION
CARLOTTENSE
KUNAE
FREBOLDI
WHITEAVESI
IMLAYI
E65-68
ET5
E62-64
E61
E59
E55
E54
E50
E46
ET4
E44
E42
ET3
E38
E34
E32
E30
E26
ET2
E24
E21
E19
E17
E16
E14
E12
ET1
E11
E10
E09
E08
E07
E05
E04
E02
E01
0
10
20
30
40
50
60
70
80
90
100
SECTION E : MAUDE ISLAND

Text-figure 11.—Lithostratigraphy and fossil localities of section E, Fannin Bay, southeast Maude Island. See Text-figure 6 for legend and Text-figure 20 for the fauna present.


LITHOSTRATIGRAPHIC UNIT
THICKNESS (METRES)
LITHOLOGY
IN SITU LOCALITIES
TALUS SAMPLE
ZONE
FANNIN FORMATION
FANNIN FORMATION : RENNELL JUNCTION MEMBER
GHOST CREEK FORMATION
KUNAE
FREBOLDI
WHITEAVESI
?
F12
F11
F10
F09
F08
FT2
F07
F06
F04
F03
F02
FTI
F01
0
10
20
30
40
50
SECTION F : ROAD 19 QUARRY

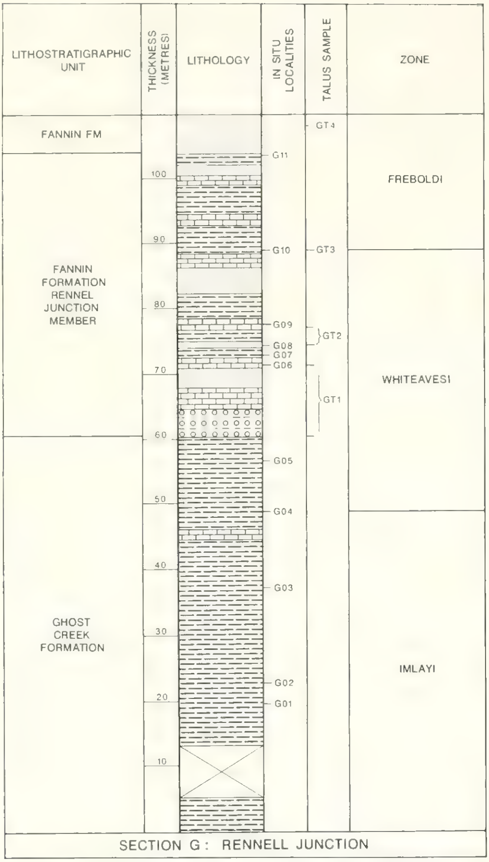
Text-figure 12.—Lithostratigraphy and fossil localities of section F, the Forest Service Road 19 Quarry. See Text-figure 6 for legend and Text-figure 21 for the fauna present.

into the overlying Whiteavesi Zone. The long-ranging genus *Metaderoceras* is represented by the distinctive *M. evolutum* with its long spines and often looped, striate ribs.

The Whiteavesi Zone fauna is considerably more diverse and characterized by a profusion of acanthopleuroceratids, the first appearance of *Dubariceras (D. silviesi)* and the occurrence of coarse ribbed, robust forms of *Metaderoceras*. In the Freboldi Zone, above the range of the acanthopleuroceratids, diversity drops again to levels comparable with the Imlayi Zone but, in marked contrast to the Imlayi Zone, the Freboldi Zone is amongst the thinnest Pliensbachian zones recognized in the Queen Charlotte Islands. *Dubariceras freboldi* occurs throughout the zone and in the upper part of its range it frequently occurs with species of *Reynesoceras*, most of which range up into the Kunae Zone.

The similarly thin Kunae Zone is remarkable for its quantum jump in diversity to the highest level seen in the Pliensbachian. Some of the increase is accomplished by the appearance of a diverse suite of *Fanninoceras* species but most is caused by the appearance and rapid diversification of the hildoceratids and a proliferation of dactylioceratids ranging up from the Freboldi Zone.

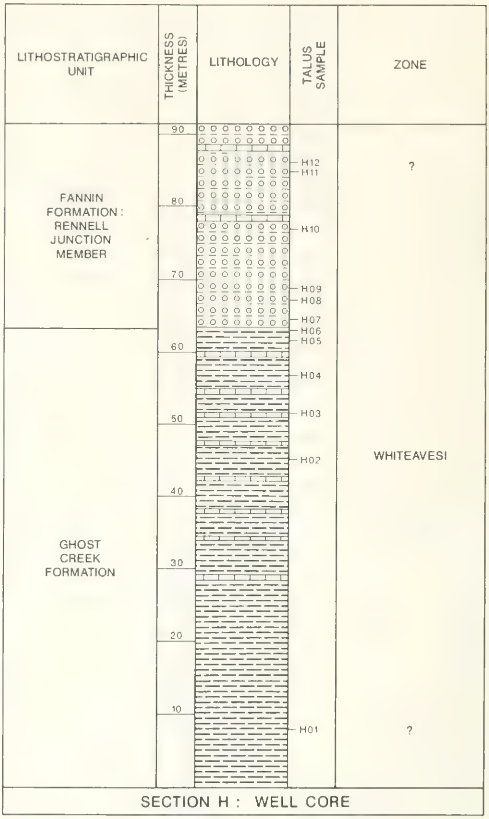
The upper part of the Fannin Formation yields three faunal associations that represent the Pliensbachian-Toarcian transition. Species of *Lioceratoides* and *Protogrammoceras* are present throughout. The lowest association (Carlottense Zone, Sections B and E) is considered Pliensbachian based on the presence of species of *Amaltheus, Arieticeras* and *Fanninoceras;* the anomalous presence of the typically Toarcian *Tiltoniceras* marks the earliest known occurrence of this genus. This association is not thought to be the result of condensing, in spite of its stratigraphic position at the top of a coarsening upwards sequence, because it occurs at different levels over a significant stratigraphic interval,


LITHOSTRATIGRAPHIC UNIT
THICKNESS (METRES)
LITHOLOGY
IN SITU LOCALITIES
TALUS SAMPLE
ZONE
FANNIN FM
FANNIN FORMATION RENNEL JUNCTION MEMBER
GHOST CREEK FORMATION
100
90
80
70
60
50
40
30
20
10
G11
G10
G09
G08
G07
G06
G05
G04
G03
G02
G01
GT4
GT3
GT2
GT1
FREBOLDI
WHITEAVESI
IMLAYI
SECTION G : RENNELL JUNCTION

Text-figure 13.—Lithostratigraphy and fossil localities of section G, Rennell Junction. See Text-figure 6 for legend and Text-figure 22 for the fauna present.

both here and elsewhere in North America (Thomson and Smith, 1992).

A middle association consisting only of species of *Lioceratoides* and *Protogrammoceras* is of uncertain position but is included within the Carlottense Zone of the Pliensbachian because of the absence of *Dactylioceras* (localities D24, D25 and I03). The highest association (localities D26 and D27) includes species of *Lioceratoides, Protogrammoceras* and *Tiltoniceras*; it is unequivocally Toarcian since it also includes *Dactylioceras* and, slightly higher, in the uppermost Fannin Formation, a representative of *Taffertia* (Jakobs *et al.*, 1994b).

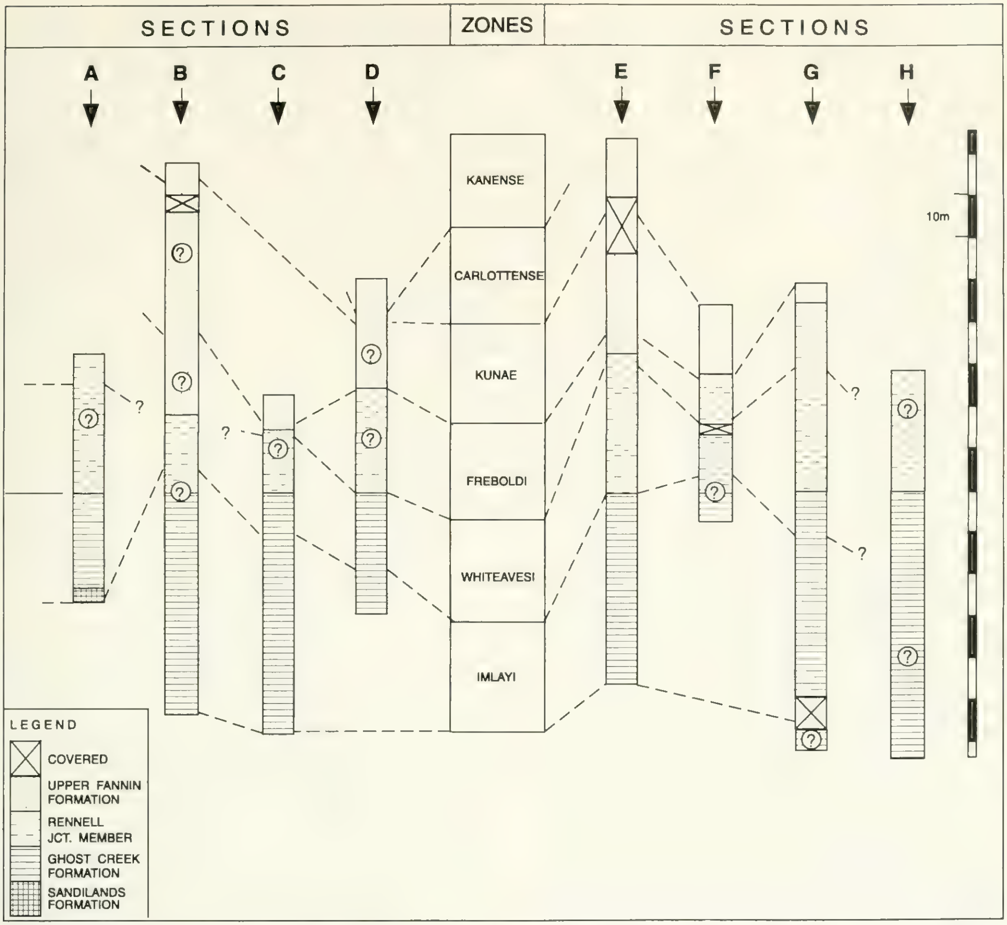

LITHOSTRATIGRAPHIC UNIT
THICKNESS (METRES)
LITHOLOGY
TALUS SAMPLE
ZONE
FANNIN FORMATION: RENNELL JUNCTION MEMBER
GHOST CREEK FORMATION
90
80
70
60
50
40
30
20
10
H12
H11
H10
H09
H08
H07
H06
H05
H04
H03
H02
H01
?
WHITEAVESI
?
SECTION H : WELL CORE

Text-figure 14.—Lithostratigraphy and fossil localities of Well Core H. See Text-figure 6 for legend and Text-figure 23 for the fauna present.

SYSTEMATIC PALEONTOLOGY

INTRODUCTION

Taxonomic groups are held to have a common ancestry (Donovan, 1994). Ammonoids are notorious for heterochronous homeomorphy and therefore it is important that before a specimen is identified, its age is constrained as closely and confidently as possible by co-occuring and stratigraphically subjacent and superjacent assemblages. For Jurassic ammonoids, septal sutures are of utility at high taxonomic levels, notably in the case of the Queen Charlotte Islands' fauna for distinguishing phylloceratids with their phylloid lobes, from the ammonites proper. Families represent distinct changes in morphology, usually involving shell geometry and features of the venter. Genera are inter-


SECTIONS
ZONES
SECTIONS
A
B
C
D
E
F
G
H
KANENSE
CARLOTTENSE
KUNAE
FREBOLDI
WHITEAVESI
IMLAYI
10m
?
LEGEND
COVERED
UPPER FANNIN FORMATION
RENNELL JCT. MEMBER
GHOST CREEK FORMATION
SANDILANDS FORMATION

Text-figure 15.—Correlation of Pliensbachian units in the Queen Charlotte Islands. Correlation lines are drawn at the incoming of faunas and question marks indicate no, or poor biostratigraphic control.

preted to represent lineages; they are characterized by their shell geometry, whorl shape, ornamentation and consistent patterns of ontogenetic change. Subgeneric status is accorded to derivative forms showing new or incipient features that lead to new taxa. The recognition of species usually requires a large enough sample to demonstrate discontinuous variation, particularly involving whorl shape and ornamentation. When extreme variations are stratigraphically or geographically limited they may be designated as subspecies. We do not recommend the use of this taxonomic level even though we have occasionally employed subspecies erected by others. We suspect that widespread sampling would demonstrate a morphological spectrum that is more continuous in space and time than is presently evident.

Our use of open nomenclature essentially follows Bengston (1988). The term "*aff.*" denotes a new species that we cannot name because of small sample size, stratigraphic uncertainties, or other ambiguities. "*Confer*" meaning "to compare" and abbreviated "*cf.*", is used to denote a provisional identification when poor preservation precludes confidence. We use a question mark to denote uncertainty, usually at the genus-level.

SECTION A: KUNGA ISLAND

	LOCALITIES												
TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13
Reynesoceras italicum													●
Metaderoceras spp.													●
Dubariceras freboldi												●	●
Metaderoceras talkeetnaense											●		
Metaderoceras? spp.									●				
Tropidoceras cf. flandrini flandrini								●					
Tropidoceras spp.							●						
Acanthopleuroceras whiteavesi						●							
Acanthopleuroceras thomsoni						●	—	●	—	●			
Tropidoceras actaeon				●	●								
Metaderoceras evolutum			●	—	●								
Tropidoceras cf. *erythraeum*		●											
Acanthopleuroceras cf. *whiteavesi*	●	●											
Tropidoceras cf. *masseanum rotunda*	●												
ZONE	W	W	W	W	W	W	W	W	W	W	?	F	F

Text-figure 16.—The ammonite fauna and biostratigraphy of section A. See Text-figure 7 for stratigraphic details and Text-figure 6 for the legend.

Throughout the systematics section under "Occurrence" there is a summary of the age of a species in other parts of the world using the European primary standard zonation (Dean *et al.*, 1961). Occurrences in North America other than in the Queen Charlotte Islands are also listed and referred to the North American standard zonation (Smith *et al.*, 1988). The sections headed "Localities" and "Age" only list locality numbers and North American zone assignments for the Queen Charlotte Island ammonites described in this report.

It is not always possible to be precise about the number of specimens representing a species because earlier collections sometimes contain fragments of inner and outer whorls that may or may not belong to the same specimen. On several occasions we have been able to assemble an individual from fragments collected by different people at different times. In spite of this imprecision, the data give a reasonably accurate impression of the relative abundance of species in the Queen Charlotte Islands.

Terminology and Abbreviations

The morphologic terminology used in the systematic descriptions follows that of Smith (1986). All measurements are in millimeters with approximate figures preceded by "c" (*circa*). The abbreviations denoting the measurements used are defined as follows:

D = shell diameter
UD = umbilical diameter at diameter D
U = (UD/D) × 100
WH = whorl height at diameter D
WHD = (WH/D) × 100
WW = whorl width at diameter D
WWD = (WW/D) × 100
WWWH = (WW/WH) × 100

The following parameters are counted on the half whorl terminating at the shell diameter or umbilical diameter indicated:

PRHW = primary ribs per half whorl
SRHW = secondary ribs per half whorl
THW = tubercles per half whorl.

The mean and standard deviation are given for standardized measurements (U, WWD, WHD and WWWH) unless there is a marked change during ontogeny or the dataset is small. Approximate figures are not used in the calculations.

All fossil material referred to in this report is housed in the type collection of the Geological Survey of Canada in Ottawa, hence each specimen is assigned a Geological Survey of Canada (GSC) type number.

SYSTEMATICS

Class **CEPHALOPODA** Cuvier, 1797

Order **AMMONOIDEA** Zittel, 1884

Suborder **PHYLLOCERATINA** Arkell, 1950

Family **PHYLLOCERATIDAE** Zittel, 1884

Genus **PHYLLOCERAS** Suess, 1865

Type species.—Ammonites heterophyllus J. Sowerby, 1820, pl. 226 designated by Suess (1865, p. 76).

SECTION B: LOUISE ISLAND

TAXA	LOCALITIES 1	2	T1	3	4	5	6
Tiltoniceras antiquum							●
Protogrammoceras (P.) aequiondulatum							●
Fanninoceras (Fanninoceras) carlottense							●
Reynesoceras mortilleti						●	
Reynesoceras spp						●	
Polymorphites confusus					●		
Gemmellaroceras aenigmaticum					●		
Dubariceras silviesi					●		
Acanthopleuroceras thomsoni					●		
Acanthopleuroceras whiteavesi				●			
Miltoceras aff. *sellae*			○				
Metaderoceras spp			○				
Metaderoceras evolutum			○				
Pseudoskirroceras imlayi	●	●	○				
ZONE	I	I	I	W	W	K	C

Text-figure 17.—The ammonite fauna and biostratigraphy of section B. See Text-figure 8 for stratigraphic details and Text-figure 6 for the legend.

Remarks.—Compressed involute forms with very fine ornamentation that is not visible on internal molds.

Age and distribution.—A long-ranging genus (Sinemurian to Valanginian) that is cosmopolitan in its distribution but becomes locally abundant in the circum-Mediterranean region.

Phylloceras bonarellii Bettoni, 1900
Plate 1, figure 1;
Text-figures 25c, 26b

SECTION C: CUMSHEWA INLET

TAXA	LOCALITIES T1	1	T2	2	3	4	5
Fanninoceras (Fanninoceras) fannini						●	
Metaderoceras? aff. *mouterdei*					●		●
Metaderoceras talkeetnaense					●		
Dubariceras freboldi					●		
Tropidoceras masseanum rotunda				●			
Acanthopleuroceras cf. *whiteavesi*				●			
Acanthopleuroceras sp.			○				
Tropidoceras spp.	○	●					
Pseudoskirroceras imlayi		●					
Miltoceras sp		●					
Miltoceras aff. *sellae*	○						
ZONE	I	I	W	W	F	K	C

Text-figure 18.—The ammonite fauna and biostratigraphy of section C. See Text-figure 9 for stratigraphic details and Text-figure 6 for the legend.

Phylloceras n. sp. indet. Gemmellaro, 1884, p. 176, pl. 2, figs. 11, 12.
Phylloceras zetes d'Orbigny. Fucini, 1900, p. 4, pl. 1, fig. 4.
Phylloceras bonarellii Bettoni, 1900, p. 41, pl. 3, fig. 9; Fucini, 1901b, p. 38, pl. 6, fig. 3; Pia, 1913, p. 364, pl. 13, fig. 4.
Phylloceras cf. *bonarellii* Bettoni. Monestier, 1934, p. 13, pl. 9, figs. 20, 22; pl. 11, fig. 21.
Zetoceras bonarellii (Bettoni). Wiedenmayer, 1977, p. 22, pl. 6, fig. 2.

Description.—Involute, compressed form with a rounded umbilical shoulder, flat subparallel flanks, and a broadly rounded venter. The figured specimen is completely septate so that a fairly large size was reached.

SECTION D: WHITEAVES BAY

TAXA	LOCALITIES 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	T1	T2	24	25	26	27
Tiltoniceras antiquum																									○				●
Lioceratoides (L.) sp juv																									○			●	
Dactylioceras kanense																												●	●
Protogrammoceras (P.) skidegatense																										●	●		
Protogrammoceras (P.) kurrianum																										●			
Protogrammoceras (P.) cf *paltum*																										●	●	●	●
Lioceratoides (Pacificeras) propinquum																									○	●	●	●	●
Lioceratoides (Pacificeras) angionus																										●			
Lioceratoides (L.) allifordense																									○	●		●	
Lioceratoides (L.) maurelli																									○				
Reynesoceras ragazzonii																								○					
Arieticeras lupheri																								○					
Reynesocoeloceras mortilleti																						●		○					
Arieticeras cf *micrasterias*																						●							
Reynesoceras colubriforme																					●								
Protogrammoceras (Matteiceras) cf *diornatum*																				●									
Phylloceras sp																				●									
Leptaleoceras sp																				●			●	○					
Fontanelliceras sp																				●		●							
Fanninoceras (Fanninoceras) fannini																				●									
Fanninoceras (Charlotticeras) maudense																				●									
Fieldingiceras pseudofieldingii																			●	●									
Metaderoceras talkeetnaense																●	●	●											
Dubariceras freboldi													●	●	●			●											
Phylloceras bonarellii								●												●									
Tropidoceras masseanum rotunda						●	●	●		●	●																		
Tropidoceras flandrini flandrini				●			●																						
Tropidoceras actaeon			●		●	●	●	●		●	●	●																	
Metaderoceras evolutum			●		●		●	●	●	●																			
Acanthopleuroceras whiteavesi		●					●				●																		
Tropidoceras sp 1	●																												
Tropidoceras flandrini obtusa	●							●																					
ZONE	I?	W	W	W	W	W	W	W	W	W	W	W	F	F	F	F	F	F	K	K	K	K	K	K	K	C	C	T	T

Text-figure 19.—The ammonite fauna and biostratigraphy of section D. See Text-figure 10 for stratigraphic details and Text-figure 6 for the legend.

SECTION F: ROAD 19 QUARRY

	LOCALITIES													
TAXA	1	T1	2	3	4	5	6	7	T2	8	9	10	11	12
Fuciniceras? sp									○					●
Leptaleoceras? sp									○				●	
Reynesocoeloceras? sp											●			
Reynesocoeloceras mortilleti									○					
Reynesoceras sp									○					
Protogrammoceras (Protogrammoceras) sp									○	●	—	●		
Protogrammoceras (Matteiceras) cf. *diornatum*									○					
Phylloceras bonarellii									○					
Genus and species indet.									○					
Liparoceras (Becheiceras) bechei									○					
Fieldingiceras sp.									○					
Fieldingiceras pseudofieldingii									○					
Fanninoceras (Fanninoceras) kunae									○					
Arieticeras sp.									○					
Amaltheus stokesi									○					
Fanninoceras (Fanninoceras) fannini								●	○					
Fanninoceras (Fanninoceras) spp.							●	—	—	●				
Dubariceras freboldi		○			●	●	●							
Reynesocoeloceras cf. *incertum*			●											
Metaderoceras talkeetnaense		○	●											
Metaderoceras mouterdei		○	●											
Reynesocoeloceras grahami		○												
Phylloceras spp		○	●	●										
Oistoceras compressum		○	●											
Gemmellaroceras spp		○												
Dubariceras silviesi		○												
Tropidoceras actaeon	●													
ZONES	W	F	F?	F?	F	F	F	K	K	K	K	K	K	---

Text-figure 21.—The ammonite fauna and biostratigraphy of section F. See Text-figure 12 for stratigraphic details and Text-figure 6 for the legend.

Type material.—Lectotype: Bettoni, 1900, pl. 3, fig. 9 designated by Fantini Sestini, 1974, p. 226.

Material.—Approximately 14 specimens, only one of which is well preserved, in siltstone and fine grained calcareous sandstone of the Ghost Creek and Fannin formations.

Measurements.—See Table 1.

Occurrence.—In the Old World this species occurs in the Tethyan faunas of southern Europe where it ranges from the Jamesoni to the Spinatum Zone (Fantini Sestini, 1974; Wiedenmayer, 1977;).

Localities.—DO8, D20, E27, ET4, FT2, GT3, G02, I14.

Age.—Imlayi to Kunae Zone (Pliensbachian).

Phylloceras sp.

Plate 1, figures 2, 3; Text-figures 25a-b, 26a

Partschiceras? Imlay, 1968, p. C26, pl. 1, figs. 14, 15.
Phylloceras sp. Thomson and Smith, 1992, pl. 3, fig. 5.

Description.—Very involute forms with a compressed whorl section. The flanks are gently convex to almost flat and diverge weakly towards the venter. The venter is broad and gently rounded. The specimens are all smooth internal molds. First and second lateral saddles triphyllic.

Material.—Eleven internal molds in fine grained calcareous sandstone of the Rennell Junction Member of the Fannin Formation.

Measurements.—See Table 2.

Discussion.—This form shows some similarities to the species *Phylloceras frondosum* (Reynès) and *P. waehneri* (Gemmellaro). *P. frondosum* is slightly less involute with a narrower venter and *P. waehneri* has more rounded flanks and a narrower venter.

Occurrence.—*P. frondosum* ranges throughout the Pliensbachian; *P. waehneri* has only been reported from the Lower Pliensbachian (Fantini Sestini, 1974).

Localities.—D20, ET1, E27, E55, FT2, F02.

Age.—Whiteavesi and Kunae zones (Pliensbachian).

Family **JURAPHYLLITIDAE** Arkell, 1950

Genus **TRAGOPHYLLOCERAS** Hyatt, 1900

Phyllolobites Vadász, 1907, p. 352.

Type species.—*Ammonites heterophyllus numismalis* Quenstedt, 1845, p. 100, pl. 6, figs. 4a,b; 5a,b, by original designation (Hyatt, 1900, p. 568).

SECTION G: RENNELL JUNCTION

	LOCALITIES														
TAXA	1	2	3	4	5	T1	6	7	8	9	T2	10	T3	11	T4
Liparoceras (Becheiceras) bechei															○
Fanninoceras (Fanninoceras) kunae															○
Fanninoceras (Fanninoceras) fannini															○
Fanninoceras (Fanninoceras) crassum															○
Arieticeras disputabile															○
Amaltheus stokesi															○
Reynesocoeloceras mortilleti													○		
Reynesocoeloceras grahami													○		
Gemmellaroceras aenigmaticum													○		
Dubariceras freboldi											○	●	○	●	
Metaderoceras mouterdei										●			○		
Tropidoceras masseanum rotunda							●						○		
Metaderoceras talkeetnaense						○	●	●	●	●	○		○		
Metaderoceras evolutum						○	●								
Reynesocoeloceras spp						○									
Dubariceras silviesi						○							○		
Acanthopleuroceras thomsoni						○							○		
Tropidoceras actaeon					●	○	—	—	—	●					
Acanthopleuroceras whiteavesi				●											
Tropidoceras flandrini flandrini			●	●											
Polymorphites confusus	●	—	●	—	●	—	—	—	—	●					
Phylloceras bonarellii		●											○		
Tropidoceras sp. 1	●														
Tropidoceras cf. *erythraeum*	●	●	●												
Pseudoskirroceras imlayi	●	●	●												
Miltoceras aff. *sellae*	●	●	●												
Gemmellaroceras cf. *alloplocum*	●	—	●	●											
ZONES	I	I	I	W	W	W	W	W	W	W	---	F	---	F	K

Text-figure 22.—The ammonite fauna and biostratigraphy of section G. See Text-figure 13 for stratigraphic details and Text-figure 6 for the legend.

Remarks.—Phylloceratines with compressed whorl sections and an open umbilicus. Constrictions are apparent on internal molds. Ornamentation is flexuous and strengthens ventrally. The genus has been discussed by Howarth and Donovan (1964), and Meister (1986).

Age and distribution.—The family Juraphyllitidae in Europe is predominantly Tethyan in its distribution with the exception of *Tragophylloceras* which is characteristic of, but not restricted to, northwest Europe. The genus ranges from the Jamesoni to the Margaritatus Zone.

Tragophylloceras new species?
Plate 1, figure 6

Tragophylloceras sp. Imlay, 1968, p. C26, pl. 1, figs. 10, 11.

Description.—Involute form with a compressed whorl section. The umbilical wall is very low and steep, the umbilical shoulder abrupt, the flanks flat and the venter

SECTION H: WELL CORE

	LOCALITIES											
TAXA	1	2	3	4	5	6	7	8	9	10	11	12
Metaderoceras talkeetnaense										●	●	●
Acanthopleuroceras thomsoni								●	●			
Tropidoceras flandrini flandrini				●								
Tropidoceras actaeon		●	●	—	●	●	●					
Polymorphites confusus	●											
ZONE	---	W?	W?	W?	W?	W?	W?	W	W	---	---	---

Text-figure 23.—The ammonite fauna and biostratigraphy of well core H. See Text-figure 14 for stratigraphic details and Text-figure 6 for the legend.

ISOLATED LOCALITIES

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Acanthopleuroceras thomsoni	○	●														●	
Acanthopleuroceras whiteavesi																●	
Arieticeras disputabile														●			
Arieticeras lupheri						●											
Arieticeras aff. *algovianum*														●			○
Arieticeras aff. *domarense*						●											○
Arieticeras cf. *micrasterias*																	○
Arieticeras cf. *ruthenense*						●								●			
Cymbites centriglobus														●			
Cymbites laevigatus														●			
Dubariceras freboldi	○						●								●		
Dubariceras silviesi	○	●					●										
Fanninoceras (Fanninoceras) carlottense						●											
Fanninoceras (Charlotticeras) carteri						●	●							●			
Fanninoceras (Fanninoceras) fannini						●	●										○
Fanninoceras (Fanninoceras) kunae						●											
Fanninoceras (Charlotticeras) maudense						●											
Fieldingiceras pseudofieldingii						●	●										
Fontanelliceras sp														●			
Fuciniceras aff. *intumescens*						●											
Fuciniceras cf. *targionii*																	○
Gleviceras? sp		●															
Leptaleoceras compressum						●											
Leptaleoceras aff *accuratum*																	○
Leptaleoceras sp						●								●			
Lioceratoides (L.) allifordense			●														
Lioceratoides (Pacificeras) propinquum			●									●					
Metaderoceras evolutum								●								●	
Metaderoceras mouterdei		●															
Metaderoceras talkeetnaense		●					●								●		
Phricodoceras cf. *taylori*								●									
Phylloceras bonarellii														●			
Protogrammoceras (Matteiceras) cf diornatum						●											
Protogrammoceras (P.) cf *paltum*			●														
Protogrammoceras (P.) sp							●										
Pseudoskirroceras imlayi								●	●	●	●						
Reynesoceras colubriforme							●							●			
Reynesoceras italicum					●	●											
Reynesoceras ragazzonii						●											
Reynesocoeloceras mortilleti						●									●		
Reynesocoeloceras spp		●															
Tropidoceras actaeon		●															
Tropidoceras flandrini flandrini								●									
Tropidoceras flandrini obtusa								●									
Tropidoceras masseanum rotunda		●															
Tropidoceras cf. *erythraeum*								●	●	●	●						
Tropidoceras aff *rursicosta*								●			●		○				
Tropidoceras n sp 1		●															
Tropidoceras sp. 1				●				●			●						
ZONE	---	W	C	--	K?	K	F-K	I	I	I	I	C	I	K	F	W	K
LITHOLOGIC UNIT	R	R	Fa	G	Fa	Fa	R-Fa	G	G	G	G	Fa	G	Fa	R	G	Fa

Text-figure 24.—The ammonite fauna found at isolated localities on southern Graham Island.

narrow. Weak, broad primary ribs arise low on the flank and trend gently prorsiradiately to the upper quarter of the flank where numerous fine secondary ribs arise and the ribbing flexes slightly more prorsiradiately onto the venter. The phylloceratine septal suture line is partially exposed at the largest shell diameter where the shell has been removed.

Material.—One specimen collected from calcareous sandstone of the Fannin Formation.

Measurements.—See Table 3.

Discussion.—This phylloceratine is placed in *Tragophylloceras* because of its narrow whorl section, its fairly open umbilicus and its costation. This species is also known from a bed of the Kunae Zone in Oregon (Imlay, 1968). As Imlay remarked, the species shows some similarities to the European forms *T. loscombi* and *T. undulatum.* The differences, however, are such that the North American specimens should be tenta-

Table 1.—Measurements of *Phylloceras bonarellii* Bettoni, 1900. All measurements are in mm.

specimen no.	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WW-WH*
GSC 98693	51.6	5	9.7	16.7	32.4	28.4	55	58.8

tively regarded as a new species that can only be properly described when more material has been collected.

Occurrence.—In Europe, *T. loscombi* is the only species of *Tragophylloceras* to persist into the Upper Pliensbachian (Howarth and Donovan, 1964; Meister, 1989). The two specimens of *Tragophylloceras* now known from North America (from eastern Oregon and the Queen Charlotte Islands) are both of probable Late Pliensbachian age.

Locality.—ET4.

Age.—probably Kunae Zone (Late Pliensbachian)

Suborder **AMMONITINA** Hyatt, 1889

Superfamily **PSILOCERATACEAE** Hyatt, 1867

Family **CYMBITIDAE** Buckman, 1919

Genus **CYMBITES** Neumayr, 1878

Metacymbites Spath, 1923, p. 76.

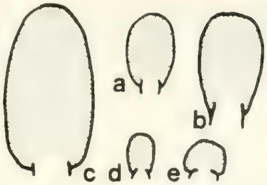
Type species.—*Ammonites globosus* Schubler *in* Zieten, 1832, p. 37, pl. 28, fig. 2 by original designation (Neumayr, 1878, p. 64).

Remarks.—Small involute to midvolute forms, with depressed or rounded whorl section. Smooth or very weakly ornamented. The last whorl commonly egresses and the aperture may be constricted and bear a rostrum. Septal suture simple.

Age and distribution.—The genus has been reported from rocks that range in age from the Sinemurian to Pliensbachian. Often locally abundant at a given horizon, it has been previously reported from Great Britain (Donovan, 1957), Germany (Schindewolf, 1961), Italy (Fucini, 1899), Portugal (Mouterde, Dommergues, and Rocha, 1983), Switzerland (Bettoni, 1900), France (Monestier, 1934), and the United States (Imlay, 1968). The genus appears to have been geographically more widespread in the Pliensbachian than the Sinemurian.

Table 2.—Measurements of *Phylloceras* sp. All measurements are in mm.

specimen no.	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WW-WH*
GSC 98575	22.4	1.5	6.7	9.5	42.4	12.3	54.9	77.2
GSC 98574	18.3	1.2	6.6	c7.8	42.6	10.5	57.4	c74.3



Text-figure 25.—Whorl shape cross-sections for species of the Phylloceratidae and Cymbitidae. Figures are natural size unless otherwise indicated. a-b. *Phylloceras* sp. (a. GSC 98574; b. GSC 98575); c. *Phylloceras bonarellii* Bettoni, 1900 (GSC 98693); d. *Cymbites laevigatus* (J. de Sowerby, 1827) (GSC 98580) (× 1.3); e. *Cymbites centriglobus* (Oppel, 1862) (GSC 98577) (× 1.3).

Cymbites centriglobus (Oppel, 1862)

Plate 1, figures 7–9,
Text-figures 25e, 26d

Ammonites globosus Oppel, 1853, p. 95, pl. 3, fig. 7; Quenstedt, 1856, p. 172, pl. 21, figs. 8, 9; 1885, p. 336, pl. 42, figs. 29, 30, 32–36.

Ammonites centriglobus Oppel, 1862, p. 140.

Cymbites centriglobus (Oppel). Fucini, 1900, p. 19, pl. 3, figs. 5, 6; Schindewolf, 1961, p. 216, pl. 31, figs. 1–18; Schlegelmilch, 1976, p. 52, pl. 22, fig. 3; Mouterde, Dommergues, and Rocha, 1983, p. 194, pl. 12, figs. 11–13; Meister, 1986, p. 64, pl. 11, fig. 5; 1989, p. 34, pl. 3, fig. 9.

Agassiceras centriglobum (Oppel). Bettoni, 1900, p. 52, pl. 8, fig. 4; Monestier, 1934, p. 27, pl. 3, figs. 4–11.

Metacymbites centriglobus (Oppel). Spath, 1938, p. 95, pl. 10, fig. 8; pl. 11, figs. 6–8; Howarth, 1957, p. 196, pl. 17, figs. 3, 4.

Metacymbites? cf. *M. centriglobus* (Oppel). Imlay, 1968, p. C27, pl. 1, figs. 1–6.

Description.—Small, involute smooth forms with a depressed whorl section. At shell diameters of approximately 8 mm, the last whorl begins to uncoil and becomes slightly compressed. The body chamber, which occupies about half a whorl at maturity, terminates in a constriction and a broad rostrum.

Type material.—Quenstedt (1862) established this species referring to the material figured by Oppel (1853, pl. 3, fig. 7) which subsequent workers took as the type (Schindewolf, 1961); this specimen is now considered lost. Quenstedt (1862) also referred to material figured by Quenstedt (1856, pl. 21, fig. 9; refigured in Quenstedt, 1885, pl. 42, fig. 30) when he established the species and this specimen was refigured and designated as the neotype by Schlegelmilch (1976).

Table 3.—Measurements of *Tragophylloceras* new species? All measurements are in mm.

specimen no.	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WW-WH*
GSC 98581	20.7	4	19.3	4.7	22.7	10.2	49.3	46.1

Table 4.—Measurements of *Cymbites centriglobus* (Oppel, 1862). All measurements are in mm.

specimen no.	*DMAX*	*DPHRAG*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*
GSC 98577	11.4	c7.5	10.6	3	28.3	4.9	46.2	4.6	43.4	106.5
GSC 98576	—	—	9.8	2.4	24.5	4.8	49	4.6	46.9	104.3
GSC 98578	10.9	9.0	10.9	2.9	26.6	5.0	45.9	4.5	41.2	111.1
MEAN					26.4		47		43.8	107.3
ST. DEV.					1.9		1.7		2.9	3.5

Material.—Sixteen internal molds in calcareous sandstone of the Fannin Formation.

Measurements.—See Table 4.

Discussion.—*Cymbites centriglobus* can be distinguished from *C. laevigatus,* with which it co-occurs, by its globose shell with its broad venter and depressed whorl section.

Occurrence.—The species is widely distributed in both southern and northwestern Europe where it ranges in age from the Obtusum to the Margaritatus Zone with its acme in the Margaritatus Zone. Outside Europe, the species has only been reported from the Late Pliensbachian Nicely Formation in east-central Oregon (Imlay, 1968).

Localities.—ET4, I14.

Age.—Kunae Zone (Late Pliensbachian).

Cymbites laevigatus
(J. de C. Sowerby, 1827)
Plate 1, figures 4, 5; Text-figure 25d

Ammonites laevigatus J. de C. Sowerby, 1827, p. 135, pl. 570, fig. 3.
Cymbites subcostulatus Spath, 1926, p. 170, pl. 11, fig. 3.
Cymbites laevigatus (J. de C. Sowerby). Donovan, 1957, p. 413, figs. 1–8; Schindewolf, 1961, p. 208, pl. 29, fig. 17; pl. 30, figs. 1–7; Schlegelmilch, 1976, p. 52, pl. 22, fig. 4.

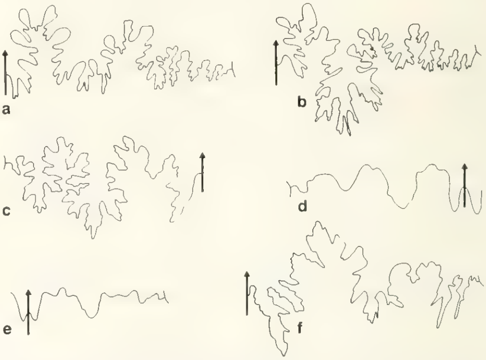
Description.—Small forms with equant to slightly depressed whorls that become compressed as the last whorl egresses. The body chamber is probably a little over half a whorl although last sutures are not clearly preserved. The mature body chamber terminates in a narrow, fairly deep constriction followed by a rostrum.

Type material.—Holotype: *Ammonites laevigatus* J. de C. Sowerby, 1827, p. 135, pl. 570, fig. 3.

Material.—Three internal molds with some shell material, preserved in calcareous sandstone of the Fannin Formation.

Measurements.—See Table 5.

Discussion.—Differs from *C. centriglobus* by its more compressed whorl section, deeper terminal constriction and a more developed rostrum.



Text-figure 26.—Traces of the septal suture for species of the Phylloceratidae, Cymbitidae, Polymorphitidae and Dactylioceratidae at whorl heights (WH) indicated. a. *Phylloceras* sp. (GSC 98575, WH = 12.3 mm); b. *Phylloceras bonarellii* Bettoni, 1900 (GSC 98693, WH = 15 mm); c. *Acanthopleuroceras whiteavesi* Smith and Tipper, 1988 (Paratype GSC 87791, WH = 15 mm); d. *Cymbites centriglobus* (Oppel, 1862) (GSC 98578, WH = 3 mm); e. *Gemmellaroceras aenigmaticum* (Gemmellaro, 1884) (GSC 98632, WH = 2.3 mm); f. *Reynesocoeloceras mortilleti* (Meneghini, 1875) (GSC 98673, WH = 8 mm).

Occurrence.—*C. laevigatus* arises in the Turneri Zone and is most common in the Upper Sinemurian but it ranges as high as the Margaritatus Zone. It is characteristic of Northwest Europe. The Queen Charlotte Islands occurrence represents the first report of this species in the circum-Pacific region.

Localities.—ET4, I14.

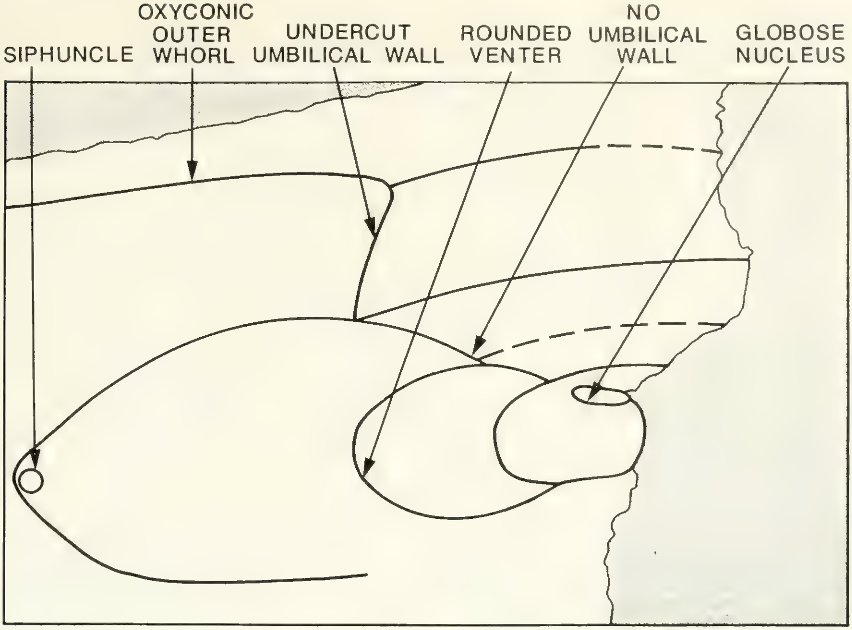
Age.—Kunae Zone (Late Pliensbachian).

Family **OXYNOTICERATIDAE** Hyatt, 1875
Genus **FANNINOCERAS** McLearn, 1930
Subgenus **FANNINOCERAS** McLearn, 1930

Type species.—*Fanninoceras fannini* McLearn, 1930, p. 4, pl. 1, fig. 3.

→

Text-figure 27.—A specimen of *Fanninoceras (Fanninoceras) fannini* broken open to show the inner whorls. Whorl shape changes from the depressed, globose inner whorls to compressed, oxyconic outer whorls. As these changes occur, the umbilical wall becomes progressively more undercut and the ribbing commonly disappears. The scale at the bottom of the photograph is in millimeters.


SIPHUNCLE
OXYCONIC OUTER WHORL
UNDERCUT UMBILICAL WALL
ROUNDED VENTER
NO UMBILICAL WALL
GLOBOSE NUCLEUS

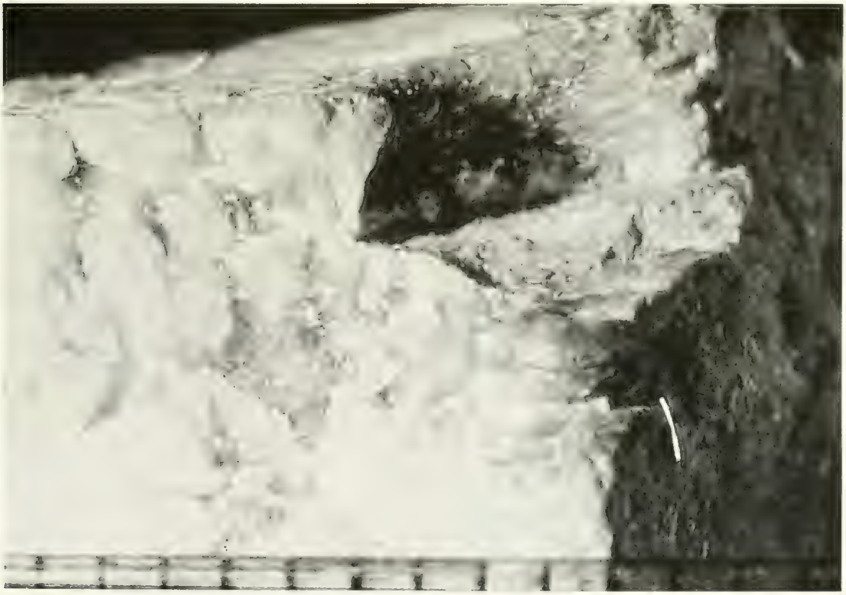
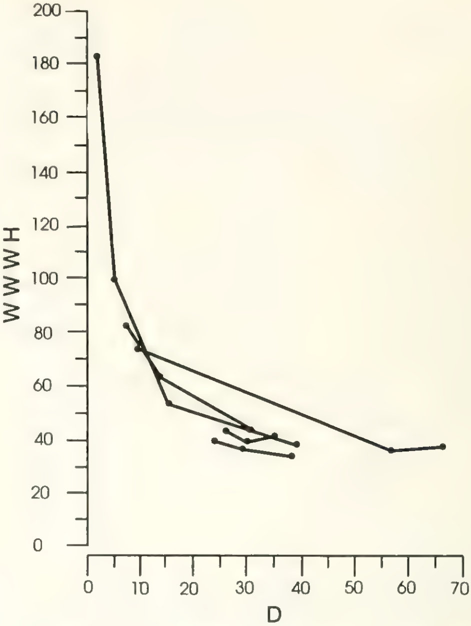


Table 5.—Measurements of *Cymbites laevigatus* (J. de C. Sowerby, 1827). All measurements are in mm.

specimen no.	*DM-AX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WW-WH*
GSC 98579	13.9	13.9	4.5	32.3	4.3	30.9	4.5	32.4	95.6
		11	2	18.2	4.2	38.1	4.3	39.1	97.7
GSC 98580	10.7	10.7	3.5	32.7	4	37.4	4	37.4	100
GSC 99018	10.5	10.5	2.5	23.8	4	38.1	4.4	41.9	90.9
MEAN				26.8		36.1		37.7	96
ST. DEV.				7		3.5		4	3.9



Text-figure 28.—The ontogeny of whorl shape in *Fanninoceras (F.) fannini*, the type species of *Fanninoceras (Fanninoceras)*, showing the characteristic change from depressed inner to compressed outer whorls (from Smith, 1986).

Remarks.—*Fanninoceras* has been considered a synonym of *Radstockiceras* Buckman, 1918, by Donovan and Forsey (1973), Donovan *et al.* (1981), and Meister (1986) but not by those workers who have actively studied eastern Pacific Lower Jurassic faunas (Frebold, 1967; Imlay, 1968, 1981; Hillebrandt, 1981, 1987; Smith, 1986; Smith and Tipper, 1986; Thomson and Smith, 1992). The reasons for its retention are based primarily on morphology but also on stratigraphic range.

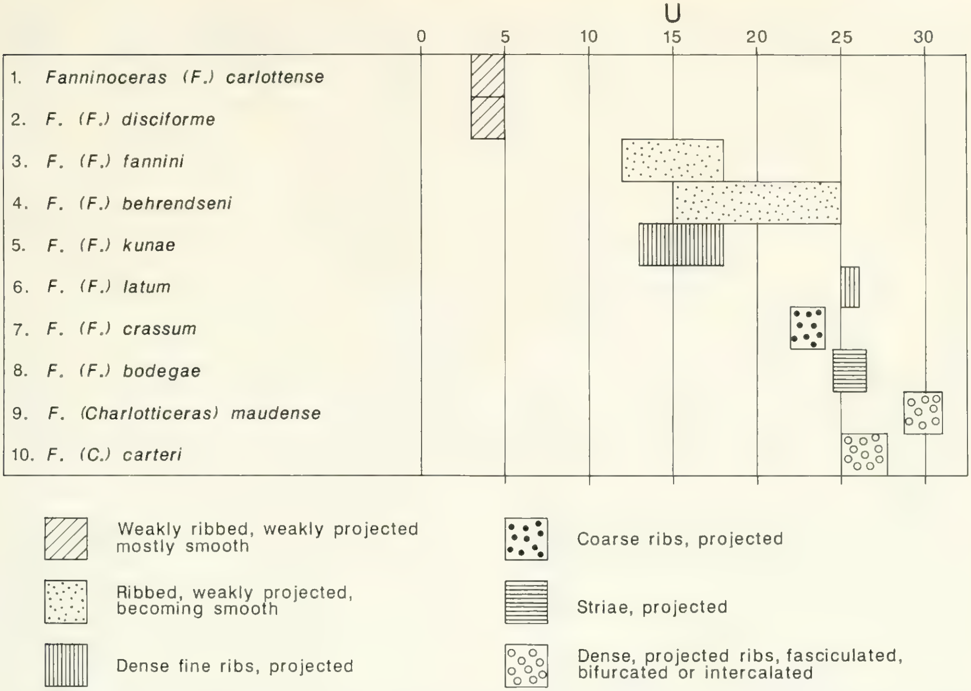
Fanninoceras undergoes a marked change in morphology during its ontogeny (Text-figs. 27 and 28). Early whorls are depressed, with a rounded venter and commonly ornamented with either coarse or fine ribbing depending on the species. At this stage the umbilical wall is low and grades evenly into the flanks. As the ribbing disappears, the whorls become compressed with a sharp venter, an undercut umbilical wall, and an acutely angled umbilical shoulder. Frebold (1967) has pointed out that the external suture of *Fanninoceras* is wider than in *Radstockiceras* and the lateral lobe consequently occupies a position nearer the middle of the flank.

Radstockiceras is a Lower Pliensbachian genus that ranges as high as the Davoei Zone in northwest Europe. The exact age of *Fanninoceras* has long been uncertain but it is now known to be characteristic of the entire Upper Pliensbachian with the first occurrence in beds that correlate approximately with the upper Davoei Zone (Smith *et al.*, 1988) and its last occurrence (one locality) in the lowest Toarcian of Chile (Hillebrandt and Schmidt-Effing, 1981, p. 30; Hillebrandt, oral commun., 1987).

We have suggested (Smith and Tipper, 1986) that *Fanninoceras* evolved from *Radstockiceras* with its origins in a form similar to *R. gemmellaroi* (see Wiedenmayer, 1977). Hillebrandt (oral commun., 1987), however, has sequences in South America that suggest an origin within the endemic genus *Eoamaltheus*. He recently figured a specimen (of *Eoamaltheus*) from the Meridianus Zone of Argentina described as intermediate between *Eoamaltheus* and *Fanninoceras* (Hillebrandt, 1990a, fig. 4.4). It is evolute and keeled, a combination of features reminiscent of the new species described herein as *Fanninoceras* (*Charlotticeras*) *carteri* and *F.* (*Charlotticeras*) *maudense*. These two species, however, do not have the tuberculate inner whorls typical of *Eoamaltheus*, they more commonly have secondary and bifurcated ribs, and they occur stratigraphically higher than species of *Eoamaltheus*. The two species are here placed in *Fanninoceras (Charlotticeras)* but it is conceivable that they belong instead to a separate genus that had its origins within *Eoamaltheus* in the south Pacific and migrated to North America in the Late Pliensbachian.

In summary, the generic features of *Fanninoceras* are the generally compressed, involute shell with an undercut umbilical wall with the shell undergoing significant morphologic changes during ontogeny. The ten species currently recognized are characterized by the combination of volution and costation as illustrated in Text-figure 29.

Age and distribution.—*Fanninoceras* is endemic to the eastern Pacific occurring from Chile and Argentina



Text-figure 29.—Typical combinations of volution and ornamentation for species of *Fanninoceras* at shell diameters greater than 20 mm. U is the ratio of umbilical diameter to shell diameter as a percentage. *Fanninoceras (F.) carlottense* includes *F. (F.) oxyconum*; *F. (F.) fannini* includes *F. (F.) dolmagii*; *F. (F.) kunae* includes *F. (F.) lowrii*.

in the south to southern Alaska in the north. In North America its first appearance is taken to mark the base of the Upper Pliensbachian and its range spans the Kunae and Carlottense zones (approximately equivalent to the uppermost Davoei to Spinatum Zone of the northwest European succession). The genus has not been reported from the Boreal craton faunas of the Fernie Group and the Arctic but it is widespread in the allochthonous Canadian terranes, the Blue and Wallowa Mountains (Oregon), and Sonomia (Nevada) (Smith and Tipper, 1986).

Most species of *Fanninoceras*, particularly the less involute and more strongly ribbed forms, occur in the Kunae Zone and its equivalents. The earliest species appears to be the South American *F. behrendseni* which is a large, relatively evolute form with strong ribbing in its early ontogeny; it appears to predate the Kunae Zone. The very involute, characteristically smooth forms such as *F. carlottense* and *F. disciforme* are more characteristic of the Carlottense Zone and its equivalents. *F. carlottense, F. fannini, F. kunae,* and *F. latum* are widely distributed along the eastern Pacific. *F. crassum* and *F. bodegae* are only known in North America whereas *F. behrendseni* and *F. disciforme* appear to be endemic to South America.

Table 6.—Measurements of *Fanninoceras* (*Fanninoceras*) *bodegae* McLearn, 1932. All measurements are in mm.

specimen no.	*DM-AX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WW-WH*
GSC 6518	29.2	27.7	7.0	25.3	5.4	19.5	12.7	45.8	42.5
		19.0	5.3	27.3	4.0	21.0	8.6	45.3	46.5

Fanninoceras (Fanninoceras) bodegae
McLearn, 1932
Plate 2, figure 2

Description.—Evolute for the genus (U>25); whorls compressed. The umbilical wall is low and slightly undercut and the flanks gently convex. The striations,

Table 7.—Measurements of *Fanninoceras* (*Fanninoceras*) *carlottense* McLearn, 1930. All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*
GSC 4878	66.5	66.5	3.5	5.3	12.3	18.5	39.6	59.6	31.1
GSC 98585	57.7	57.7	c2	c3.5	14.6	25.3	36.3	62.9	40.2
GSC 98586	c71.6	c71.6	2.5	c3.5	15	c20.9	c44	c61.5	c34.1
GSC 87807	40.8	40.8	2	4.9	10.4	25.5	24.8	60.8	41.9

which characterize the species, are visible on the upper third of the flank where they are seen to be dense and strongly projected into the venter.

Type material.—Holotype: *Fanninoceras bodegae* McLearn, 1932, p. 80, pl. 9, figs. 7–9; GSC 6518.

Material.—One specimen from the Fannin Formation.

Measurements.—See Table 6.

Discussion.—McLearn (1932) erected this species based on a single specimen that differed from all other species of *Fanninoceras* by being only moderately involute and showing striations instead of being smooth or showing costation. In terms of volution it is similar to *Fanninoceras latum* with which it could be conspecific. *F. latum* differs by having a sharper venter and ribbing which is stronger but has the same trend.

The material from Oregon identified by Imlay (1968) as *Fanninoceras* cf. *bodegae* appears to be more strongly ribbed than the type material and in many respects is similar to *Tragophylloceras* sp. described both from Oregon (Imlay, 1968) and the Queen Charlotte Islands (herein). Unfortunately a trace of the septal suture, which would settle the matter, is not available for study.

Occurrence.—Only known with certainty from the Queen Charlotte Islands; possibly present in Oregon.

Locality.—ET4.

Age.—Kunae Zone (Late Pliensbachian).

Fanninoceras (Fanninoceras) carlottense

McLearn, 1930

Plate 2, figures 3–7; Text-figures 30j, 31d

Sphenodiscus requienianus? d'Orbigny. Whiteaves, 1884, p. 248, pl. 22, fig. 4.

Fanninoceras carlottense McLearn, 1930, p. 4; 1932, p. 76; Frebold, 1967, pl. 1, fig. 1, (holotype refigured); 1970, p. 435, pl. 2, fig. 3 (holotype refigured); Blasco, Levy and Nullo, 1978, p. 425, pl. 1, fig. 4; Smith *et al.*, 1988, pl. 5, figs. 9–11.

Fanninoceras cf. *carlottense* McLearn. Imlay, 1968, p. C44, pl. 8, figs. 23, 24; 1981, p. 36 (not figured).

non *Fanninoceras* cf. *carlottense* McLearn. Hillebrandt, 1981, pl. 6, fig. 11.

Fanninoceras oxyconum Hillebrandt, 1981, p. 513, pl. 6, figs. 12–14; pl. 7, fig. 7; pl. 8, figs. 1, 2; pl. 10, figs. 9–12; Quinzio, 1987, pl. 5, fig. 1.

Fanninoceras aff. *disciforme* Hillebrandt. Pérez, 1982, pl. 18, fig. 8.

Description.—Very involute, rapidly expanding form with a compressed whorl section and an acute venter. Ornamentation is very weak consisting of broad, sometimes striate ribs that are prorsiradiate, gently flexuous on the flanks and only weakly projected onto the venter. Up to shell diameters of approximately 1 cm, the ribbing is slightly stronger and the venter more rounded than acute. At shell diameters in excess of 3 cm, the shell is usually smooth. The species reached a large size (diameters in excess of 15 cm), as suggested by many large fragments found and the fact that the holotype is completely septate. Hillebrandt (1981) figures a specimen of *F. oxyconum* (considered here a synonym of *F. carlottense*) that is completely septate at a shell diameter of 14 cm and has an expansion rate of approximately 3 suggesting a complete diameter of approximately 24 cm assuming a body chamber of half a whorl.

Type material.—Holotype: *Sphenodiscus requienianus*? d'Orbigny, Whiteaves, 1884, p. 248, pl. 22, fig. 4 by original designation (McLearn, 1930); GSC 4878.

Material.—Sixteen specimens in calcareous sandstone of the Fannin Formation.

Measurements.—See Table 7.

Discussion.—*Fanninoceras carlottense* is the most involute, the least costate, and stratigraphically the highest ranging species of *Fanninoceras* in the Queen Charlotte Islands.

Occurrence.—Reported from Argentina (Blasco *et al.*, 1978), Chile (Hillebrandt, 1981; Perez, 1982), Nevada (Smith and Tipper, 1986), Oregon (Imlay, 1968; Smith *et al.*, 1988), and Alaska (Imlay, 1981). It is characteristic of the Upper Pliensbachian, particularly the highest parts.

Localities.—B06, ET4, ET5, E63, E66, I06.

Age.—Kunae (rare) and Carlottense zones (Late Pliensbachian).

Fanninoceras (Fanninoceras) crassum

McLearn, 1932

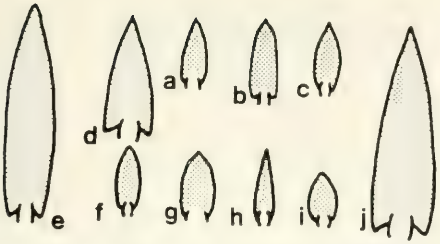
Plate 4, figures 1–4; Text-figure 30c

Fanninoceras kunae var. *crassum* McLearn, 1932, p. 78, pl. 9, figs. 1–4; Frebold, 1964b, pl. 9, fig. 4.

Fanninoceras kunae McLearn. Imlay, 1981, p. 36, pl. 7, fig. 11.

Fanninoceras crassum McLearn. Smith, Tipper, Taylor and Guex, 1988, pl. 4, fig. 5, 6.

Description.—Rapidly expanding and evolute. The venter is rounded on the nucleus (pl. 4, fig. 3c). The



Text-figure 30.—Whorl shape cross-sections for species of *Fanninoceras.* Figures are natural size unless otherwise indicated. a-b. *Fanninoceras (Charlotticeras) maudense,* n. sp. (a. Paratype GSC 98624, b. Paratype GSC 98619)(both x1.3); c. *Fanninoceras (Fanninoceras) crassum* McLearn, 1930 (GSC 98603); d-e. *Fanninoceras (Fanninoceras) fannini* McLearn, 1930 (d. Holotype GSC 9054, e. Plesiotype GSC 6495); f. *Fanninoceras (Fanninoceras) latum* McLearn, 1930 (Type GSC 98610) (x1.3); g. *Fanninoceras (Fanninoceras) kunae* McLearn, 1930 (GSC 98607); h-i. *Fanninoceras (Charlotticeras) carteri,* n. sp. (h. Holotype GSC 98614, i.Paratype GSC 98618) (both x1.3); j. *Fanninoceras (Fanninoceras) carlottense* McLearn, 1930 (Holotype GSC 4878).

outer whorls are compressed, the umbilical wall undercut, the flanks flat and the venter sharp.

The low density ribs are coarse, rectiradiate on the flanks and projected onto the venter.

Type material.—*Fanninoceras kunae* var. *crassum* McLearn, 1932; Holotype: GSC 6496, pl. 9, figs. 1–2 (refigured herein, Pl. 4, fig. 2); Paratype: GSC 6517, pl. 9, figs. 3–4 (refigured herein, Pl. 4, fig. 1).

Material.—Five specimens in calcareous sandstone of the Fannin Formation.

Measurements.—See Table 8.

Discussion.—When McLearn (1932) established the species *F. kunae* he recognized two varieties, a coarsely ribbed form he called *F. kunae* var. *crassum* and an evolute, more finely ribbed form called *F. kunae* var. *latum.* Not only are these forms morphologically distinct with no apparent intermediates, they have different geographic distributions. McLearn's varieties are therefore raised to specific status.

F. crassum is one of the more evolute species of *Fanninoceras* (Text-fig. 29) but, as the name suggests, it is most characterized by the coarseness of its ribbing.

Occurrence.—*F. crassum* is also known from the Ashcroft area (Arthur, 1985) of southern British Columbia and the Wallowa Mountains in northeastern Oregon (Smith, 1981). The forms from east-central Oregon suggested by Imlay (1968) to be *F. crassum* have a whorl section that is far too wide and a broad, rounded venter; they probably represent a new species.

Localities.—E55, ET4, GT4.

Age.—Kunae Zone (Late Pliensbachian).

Fanninoceras (Fanninoceras) fannini
McLearn, 1930
Plate 3, figures 1–12; Plate 5, figures 1, 2;
Text-figures 27, 30d–e, 31a–c

Fanninoceras fannini McLearn, 1930, p. 4, pl. 1, fig. 3; 1932, p. 72, pl. 7, figs. 7, 8; pl. 8, figs. 1–8; Frebold, 1964b, pl. 8, figs. 1, 3, 8; pl. 9, fig. 5 (type material refigured); 1967, pl. 1, figs. 2, 3 (holotype and paratype refigured); 1970, pl. 2, fig. 5 (paratype refigured); Blasco, Levi and Nullo, 1978, p. 424, pl. 1, fig. 7; Hillebrandt, 1981, pl. 6, figs. 3–5, 8–10; Pérez, 1982, pl. 18, figs. 11–13; Smith *et al.,* 1988, pl. 4, figs. 3, 4, 7.

Fanninoceras dolmagii McLearn. McLearn, 1932, p. 75, pl. 5, figs. 4, 5; Frebold, 1967, pl. 1, fig. 5 (holotype refigured).

Fanninoceras sp. Blasco, Levy and Nullo, 1978, p. 425, pl. 1, fig. 11.

Fanninoceras cf. *carlottense* McLearn. Hillebrandt, 1981, pl. 6, fig. 11.

Description.—Early whorls are depressed with a broadly arched venter and a low, gently sloping umbilical wall. Ribs are simple, strong, prorsiradiate, and weakly projected onto the venter where they quickly fade. After shell diameters of 10 to 15 mm the whorls become compressed and the ribs broaden and become more densely spaced. As growth continues, whorl compression increases, the umbilical wall becomes marked and undercut, and the ribs disappear (Text-figs. 27 and 28).

Type material.—When the species was set up it was illustrated by an inadequate sketch of the holotype (McLearn, 1930). The holotype (GSC 9054) was properly illustrated by McLearn (1932, pl. 8, figs. 1–3) and it is refigured herein (Pl. 3, fig. 2). McLearn (1932) also designated the following plesiotypes: GSC 6493 (pl. 8, fig. 4; refigured herein, Pl. 3, fig. 6); GSC 6494 (pl. 7,

Table 8.—Measurements of *Fanninoceras* (*Fanninoceras*) *crassum* McLearn, 1932. All measurements are in mm.

specimen no.	*DMAX*	*DPHRAG*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*PRHW*
GSC 6517	c26	—	24	5	20.8	5.8	24.2	10.8	45	53.7	13
GSC 6496	—	—	28.3	6.7	23.8	c5.0	c17.6	13.6	48.0	c36.8	c13
		—	24.0	5.8	24.2	c4.5	c18.7	11.8	49.2	c38.1	—
GSC 98603	24.3	24.3	24.3	5.8	23.9	5.4	22.2	10.9	44.9	49.5	15
GSC 87798	22.9	c16	21.5	4.8	22.3	5.6	26.0	9.4	43.7	59.6	13
		—	18	4.3	23.9	4.9	27.2	7.9	43.9	62.0	12

Table 9.—Measurements of *Fanninoceras* (*Fanninoceras*) *fannini* McLearn, 1930. All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*
GSC 6493	35.2+	35.2	4.7	13.3	8.7	24.7	20.3	57.8	42.9
		29.8	4.3	14.4	6.8	22.8	16.8	56.4	40.5
		25.8	4.6	17.8	6.0	23.2	13.6	52.7	44.1
GSC 6494	36.8	32.3	—	—	7.8	24.0	17.4	54.0	44.8
		14.0	3.3	23.5	4.5	32.0	7	50.0	64.3
		7.5	2.2	29.3	2.8	37.3	3.4	45.3	82.4
GSC 6495	—	66.6	7.8	11.7	14.2	21.3	36.5	54.8	38.9
		56.6	—	—	11.4	20.1	30.4	53.7	37.5
		9.4	2.8	30.0	3.6	38.2	4.8	51.0	75.0
GSC 6519[1]	34.1	34.1	6.1	17.9	7.1	20.8	18.3	53.6	38.8
GSC 9054[2]	38.5	38.5	5.2	13.5	7.3	18.9	21	54.5	34.8
		30.0	5.5	18.2	5.8	19.2	25.6	52.0	37.2
		24.2	4.8	20.0	5.0	20.6	12.3	50.8	40.7
GSC 98594	25.8	25.0	2.8	11.2	5.9	23.6	14.2	56.8	41.5
GSC 98596	12.4	12	3.0	25	3.4	28.3	4.9	40.1	69.4
GSC 98597	c52.5	51.4	6.2	12.1	12	23.3	29.5	57.4	40.7
GSC 98598	29.6	28.2	2.9	10.3	7.9	28	16.4	58.2	48.2
GSC 87799	—	—	—	—	15.7	—	39.5	—	39.7
GSC 98600	22.6	22.6	2.5	11.1	6.4	28.3	12.6	55.8	50.8

[1] Holotype of *F. dolmagii.*

[2] Holotype of *F. fannini.*

figs. 7, 8; refigured herein, Pl. 3, fig. 4); GSC 6495 (pl. 8, figs. 5–8; refigured herein, Pl. 3, fig. 1).

Material.—Approximately 65 specimens in calcareous sandstone and siltstone of the Fannin Formation.

Measurements.—See Table 9.

Discussion.—At similar shell diameters, *F. (F.) dolmagii* (holotype refigured on Pl. 3, fig. 3) is indistinguishable from *F. (F.) fannini* and the two are here considered synonyms.

In terms of volution, *F. (F.) fannini* belongs to the intermediate group of species where U=c.15 at large shell diameters. The similarly volute *F. (F.) kunae,* which also occurs in the Queen Charlotte Islands, differs by having sharper, more densely spaced ribs that project more strongly onto the venter.

Occurrence.—*F. fannini* is widely distributed in the eastern Pacific where it is most characteristic of the lower part of the Upper Pliensbachian; it is used as a zonal index in South America (Hillebrandt, 1987).

Localities.—C04, D20, ET4, ET5, E53–56, E58, E63, FT2, F07, GT4, I06, I07, I17.

Age.—Kunae Zone and rare occurrences in the Carlottense Zone (Late Pliensbachian).

Fanninoceras (Fanninoceras) kunae
McLearn, 1930
Plate 4, figures 5–8, 11, 12; Text-figure 30g

Fanninoceras kunae McLearn, 1930, p. 5, pl. 2, fig. 4; 1932, p. 77, pl. 8, figs. 11, 12; Frebold, 1967, fig. 4 (holotype refigured); Smith, Tipper, Taylor and Guex, 1988, pl. 4, figs. 1, 2 (holotype refigured).

Fanninoceras lowrii McLearn, 1930, p. 5, pl. 1, fig. 6; 1932, p. 79, pl. 9, figs. 10, 11.

non *Fanninoceras kunae* McLearn. Imlay, 1968, p. C44, pl. 8, fig. 25–32.

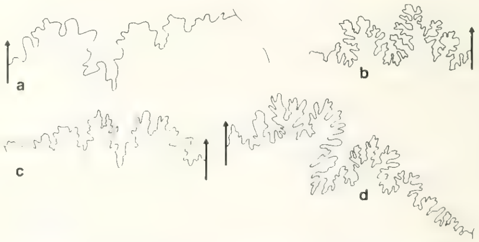
non *Fanninoceras kunae* McLearn. Imlay, 1981, p. 36, pl. 7, fig. 11.

Fanninoceras cf. *lowrii* McLearn. Hillebrandt, 1981, pl. 6, figs. 15–17.

Protogrammoceras(?) or *Fanninoceras(?)* sp. Pérez, 1982, pl. 18, fig. 4.

Description.—An involute form with an undercut to vertical umbilical wall and flat flanks. The fine ribbing is flexuous and projects onto the venter.

Type material.—Holotype: GSC 4876c figured as an inadequate sketch (McLearn, 1930, pl. 2, fig. 4); properly figured by McLearn in 1932 (pl. 8, figs. 11, 12) and refigured herein (Pl. 4, fig. 6). McLearn (1932)



Text-figure 31.—Traces of the septal suture for species of *Fanninoceras* at whorl heights (WH) indicated. a-c. *Fanninoceras (Fanninoceras) fannini* McLearn, 1930 (a. GSC 98594, WH = 6.8 mm, b. Plesiotype GSC 6495, WH = 36 mm, c. Holotype GSC 9054, WH = 14.5 mm); d. *Fanninoceras (Fanninoceras) carlottense* McLearn, 1930 (Holotype GSC 4878, WH = 36.3 mm).

Table 10.—Measurements of *Fanninoceras* (*Fanninoceras*) *kunae* McLearn, 1930. All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*PRHW*
GSC 4876c[1]	—	25.5	4.8	18.8	5.3	20.8	13.0	51.0	40.8	c19
GSC 6670[2]	—	33.5	5.5	16.4	8.6	25.7	17.5	52.2	49.1	c22
GSC 9055[3]	—	21.4	3.1	14.5	4.9	23.0	11.6	54.0	42.2	—
GSC 98607	27	27	c3.5	c13.0	6.8	25.2	15.7	58.1	43.3	c24
GSC 98608	22.4	22.4	3.2	14.3	—	—	13.3	59.4	—	25

[1] Holotype of *F. kunae.*
[2] Plesiotype of *F. kunae.*
[3] Holotype of *F. lowrii.*

described but did not figure a plesiotype (GSC 6670) which is figured herein (Pl. 4, fig. 5).

Material.—Ten specimens in calcareous sandstone of the Fannin Formation.

Measurements.—See Table 10.

Discussion.—*F. lowrii* is placed in synonymy with *F. kunae* because the only notable difference between the holotypes (Pl. 4, figs. 6 and 11) is that *F. lowrii* is more involute and the ribbing slightly less sharp. These differences, however, are not considered significant enough to warrant separation at the specific level as there are now specimens that are intermediate between these two forms both in volution and costation (Pl. 4, figs. 7 and 8). The species *Fanninoceras kunae* and *F. lowrii* were erected in the same publication (McLearn, 1930) but the name *F. kunae* has priority by virtue of being the first described in the text.

Occurrence.—*F. kunae,* the zonal index of the Kunae Zone, is known from the eastern Pacific where it characterizes the lower part of the Upper Pliensbachian (Smith *et al.,* 1988).

Localitites.—ET4, E55, E58, FT2, GT4, I06.

Age.—Kunae Zone (Late Pliensbachian).

Fanninoceras (Fanninoceras) latum
McLearn, 1930
Plate 4, figures 9, 10; Text-figure 30f

Fanninoceras kunae var. *latum* McLearn, 1930, p. 5, pl. 2, fig. 3; 1932, p. 78, pl. 9, figs. 5, 6.
Fanninoceras kunae latum McLearn. Hillebrandt, 1981, p. 513, pl. 6, fig. 6; pl. 10, fig. 6.
Fanninoceras sp. Pérez, 1982, pl. 20, fig. 10.
Fanninoceras cf. *kunae* McLearn. Hillebrandt, 1990a, pl. 4, fig. 1.
Fanninoceras latum McLearn. Thomson and Smith, 1992, p. 33, pl. 12, figs. 10, 11.

Description.—Evolute with a compressed whorl section, a low, slightly undercut umbilical wall, gently convex flanks and an acute venter. The ribbing is intermediate in coarseness between *Fanninoceras kunae* and *F. crassum*; it is gently prorsiradiate, slightly flexuous on the flanks and weakly projected. Sutures are not evident.

Type material.—Holotype: GSC 9058 figured as an inadequate sketch (McLearn, 1930, pl. 2, fig. 3); properly figured by McLearn in 1932 (pl. 9, figs. 5, 6) and refigured herein (Pl. 4, fig. 9).

Material.—Six specimens in calcareous sandstone of the Fannin Formation.

Measurements.—See Table 11.

Discussion.—McLearn's (1932) variety *Fanninoceras kunae* var. *latum* is here raised to species status because of its morphological differences compared to *F. kunae* as summarized in Text-figure 29; the two forms also have different geographic distributions. The outer whorls on both specimens of *F. latum* available for study appear to be egressing slightly and the ribs become slightly more projected indicating that it may represent a microconch.

Occurrence.—*F. latum* has been reported from the Pliensbachian of north-central British Columbia (Thomson and Smith, 1992) and Atacama, Chile (Hillebrandt, 1981).

Localities.—E50 and ET4.

Age.—Kunae Zone (Late Pliensbachian).

Fanninoceras (Fanninoceras) sp. 1
Plate 4, figure 13

Description.—Specimen GSC 98589 is small and incomplete but its early whorls show the characteristic

Table 11.—Measurements of *Fanninoceras* (*Fanninoceras*) *latum* McLearn, 1930. All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*PRHW*
GSC 9058	24.5	24.5	6.2	25.3	5.2	21.2	10.5	42.8	49.5	18
		19.5	5.2	26.6	3.8	25.3	9.2	47.2	41.3	—
GSC 98610	18.8	18.8	5	26.6	c4.4	23.4	7.8	41.5	56.4	17

Table 12.—Measurements of *Fanninoceras* (*Fanninoceras*) sp. 2. All measurements are in mm.

specimen no.	*DM-AX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WW-WH*
GSC 98613	25	25	3	12	7	28	13.5	54	51.9

ontogenetic development of *Fanninoceras* passing from a globose nucleus to a compressed stage with an undercut umbilical wall. Ribs are simple, moderately densely spaced and projected. The specimen differs from other species of *Fanninoceras* in being fairly evolute and, more significantly, in the outer non-septate whorl fragment, which has a fastigate whorl section and ribs that project onto the venter to form weak chevrons. The specimen either represents a new species or perhaps a microconch.

Material.—One specimen from the Fannin Formation.

Locality.—ET5.

Age.—Carlottense Zone (Late Pliensbachian).

Fanninoceras (Fanninoceras) sp. 2

Plate 4, figure 14

Description.—Specimen GSC 98613 is a small, completely septate specimen that is involute and compressed with a vertical umbilical wall and fairly flat flanks. It differs from other species of *Fanninoceras* in its venter which is relatively broad and blunt. Except for weak, prorsiradiate lirae visible on one part of the specimen, there is no evidence of ornamentation.

Material.—One specimen from the Fannin Formation.

Measurements.—See Table 12.

Locality.—E63.

Age.—Carlottense Zone (Late Pliensbachian).

Subgenus **CHARLOTTICERAS**, new subgenus

Type species.—*Fanninoceras (Charlotticeras) carteri,* n. sp.

Remarks.—Forms that undergo an ontogenetic change from stout inner to compressed outer whorls like other species of *Fanninoceras* but which differ in having an incipient, irregular keel and ribs divided irregularly into primaries and secondaries. It is possible that this group is derived from finely and densely ribbed forms such as *F. (F.) kunae* and *F. (F.) latum,* particularly the latter which is suitably evolute (Text-fig. 29). As discussed above, however, it is also possible that *Fanninoceras* and *Charlotticeras* had separate origins within *Eoamaltheus,* a genus endemic to the latest early Pliensbachian of South America.

Age and distribution.—This subgenus is restricted to the Kunae Zone of North America.

Table 13.—Measurements of *Fanninoceras* (*Charlotticeras*) *carteri,* new species. All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WH*	*WHD*	*PR-HW*	*SR-HW*
GSC 98614	23	20	5.5	27.5	9	45	c12	c23
GSC 98615	c23.5	16	4.4	27.5	c8.5	c53.1	c14	c27
GSC 98617	–	16	4.4	27.5	7.2	45	11	18
GSH98618	–	14	3.5	25.0	6.0	42.9	c15	18

Fanninoceras (Charlotticeras) carteri, new species

Plate 5, figures 13–15; Plate 6, figures 1–5;
Text-figure 30h–i

Description.—A midvolute form with a compressed whorl section. Until umbilical diameters of approximately 3–4 mm, the umbilical wall rounds evenly into the gently convex flanks and the venter is broadly rounded. At larger umbilical diameters the umbilical wall becomes abrupt, the flanks more flattened and the sharp venter bears a weak keel that is irregular or serrated as a result of being crossed by the ribs. Ribs are fairly sharp, irregularly fasciculated on the lower third of the flank and projected onto the venter; some intercalated ribs are evident.

Type material.—Holotype: GSC 98614 (Pl. 6, fig. 1). Paratypes: GSC 99029 (Pl. 5, fig. 13), GSC 99028 (Pl. 5, fig. 14), GSC 99026 (Pl. 5, fig. 15), GSC 98615 (Pl. 6, fig. 2), GSC 98616 (Pl. 6, fig. 3), GSC 98617 (Pl. 6, fig. 4), GSC 98618 (Pl. 6, fig. 5).

Material.—Approximately 26 specimens in calcareous sandstone of the Fannin Formation.

Measurements.—See Table 13.

Derivation of name.—This species is named in honor of Elisabeth Carter, a micropaleontologist who has made valuable contributions to our understanding of the Jurassic biostratigraphy of the Queen Charlotte Islands.

Discussion.—*Fanninoceras carteri* differs from other species of *Fanninoceras* by the fasciculation and intercalation of ribs, and the presence of a weak keel.

Occurrence.—This species is known unequivocally only from the Queen Charlotte Islands. It may also be represented in an Upper Pliensbachian ammonite assemblage from the Tulsequah area of northwestern British Columbia (Ammonite gen. et sp. indet. 1, Frebold, 1964a, p. 22, pl. 2, figs. 7–9) but the material is too poorly preserved to be confident.

Localities.—E51, E55, E57, I06, I07, I14.

Age.—Kunae Zone (Late Pliensbachian).

Fanninoceras (Charlotticeras) maudense, new species

Plate 6, figures 6–11; Text-figure 30a–b

Table 14.—Measurements of *Fanninoceras* (*Charlotticeras*) *maudense*, new species. All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WW-WH*
GSC 98619	26.3	24.5	7.0	28.6	5.0	20.4	10	50
GSC 98620	21.5	19.5	6.1	31.2	4.8	—	7.9	60.8
GSC 98622	c24	19.5	5.6	28.7	—	—	8.0	—
GSC 98623	17.5	15.8	3.7	23.4	3.8	—	7.3	52.1
GSC 98624	17.5	16.9	3.9	23.1	3.7	—	7.9	46.9

non *Fanninoceras maudense* (Whiteaves). Frebold, 1970, pl. 2, fig. 4.

Description.—The most evolute species of *Fanninoceras* yet recognized, this form possesses a smooth globose nucleus that rapidly changes its whorl shape to compressed with flat flanks and an arched venter that bears an incipient keel. The umbilical wall is low and vertical, and the umbilical shoulder is angular. Ribs are flexuous and gently prorsiradiate. They often bifurcate or are intercalated in an irregular manner forming 18 to 22 ribs per half whorl in total.

Type material.—Holotype: GSC 98620 (Pl. 6, fig. 7). Paratypes: GSC 98619 (Pl. 6, fig. 6), GSC 98621 (Pl. 6, fig. 8), GSC 98622 (Pl. 6, fig. 9), GSC 98623 (Pl. 6, fig. 10), GSC 98624 (Pl. 6, fig. 11), GSC 99029 (Pl. 5, fig. 13), GSC 99028 (Pl. 5, fig. 14), GSC 99026 (Pl. 5, fig. 15).

Material.—Thirty-four specimens in calcareous sandstone of the Fannin Formation.

Measurements.—See Table 14.

Derivation of name.—Named after Maude Island in Skidegate Inlet where some of the type material originated. The specimen *Sphenodiscus maudensis* Whiteaves, 1884 figured as *Fanninoceras maudense* (Whiteaves) by Frebold (1970, pl. 2, fig. 4) is not a *Fanninoceras* but a Cretaceous aconeceratinid (J.A. Jeletzky, written commun., 1984).

Discussion.—*F. maudense* differs from all other species of *Fanninoceras* except *F. carteri* by being more evolute, having an incipient keel and having the ribs irregularly differentiated into primaries and secondaries. *F. maudense* is slightly more evolute than *F. carteri*, its flanks flatter, the umbilical shoulder more angular and the ribs coarser.

Occurrence.—This species is only known from the Queen Charlotte Islands.

Localities.—D20, E56, E57, ET4, I06.

Age.—Kunae Zone (Late Pliensbachian).

Genus **GLEVICERAS** Buckman, 1918

Glevumites Buckman, 1918, p. 289.
Victoriceras Buckman, 1918, p. 293.
Guibaliceras Buckman, 1918, p. 293.
Tutchericeras Buckman, 1919, pl. 137A.
Riparioceras Schindewolf, 1962, p. 490.

Type species.—*Gleviceras glevense* Buckman, 1918, p. 289, by original designation. *G. glevense* is a subjective junior synonym of *G. subguibalianum* (Pia, 1914) (Bremer, 1965; Donovan and Forsey, 1973; Géczy, 1976).

Remarks.—Large forms that are closely related to *Oxynoticeras*. The venter becomes rounded with a sharp keel that is often lost on outer whorls. Whorl egression and coarsening of the ornament marks the mature state. The septal suture is complex.

Age and distribution.—Upper Sinemurian and Lower Pliensbachian of Europe, Turkey, and the east Pacific.

Gleviceras? sp.

Plate 2, figure 1

Description.—This poorly preserved, septate whorl fragment appears originally to have had a compressed whorl shape. The venter is keel-less. The simple ribs are broad and of low relief; they trend rursiradiately from the umbilical seam to the umbilical shoulder, rectiradiately across the middle of the flank and are weakly projected on the upper flank where they fade.

Material.—One fragment in sandstone of the Rennell Junction Member.

Discussion.—This specimen cannot be identified with confidence because of its poor preservation. It shows some resemblance to large coarsely ribbed species of *Gleviceras* which are most common in the Sinemurian but are known to occur as high as the Lower Pliensbachian (Géczy, 1976).

Locality.—I02.

Age.—Whiteavesi Zone (Early Pliensbachian).

Superfamily **EODEROCERATACEAE** Spath, 1929

Family **POLYMORPHITIDAE** Haug, 1887

Subfamily **POLYMORPHITINAE** Haug, 1887

Genus **GEMMELLAROCERAS** Hyatt, 1900

Tubellites Buckman, 1924, pl. 491.
Leptonotoceras Spath, 1925, p. 170.

Type species.—*Aegoceras aenigmaticum* Gemmellaro, 1884, pl. 3, figs. 12, 14, 15, by original designation (Hyatt, 1900, p. 574).

Remarks.—Small, evolute forms with a compressed whorl section and a rounded, featureless venter. Ornamentation is either subdued or the shell is smooth.

Age and distribution.—*Gemmellaroceras* has been reported most frequently from circum-Mediterranean countries where it is characteristic of the Jamesoni and Ibex zones (Géczy, 1976; Braga, Comas-Rengifo, Goy

Table 15.—Measurements of *Gammellaroceras senigmaticum* (Gemmellaro, 1884). All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*
GSC 98631	11.0	11.0	5.2	47.3	2.6	23.6	2.6	23.6	100
GSC 98632	13.0	12.1	6.5	53.7	2.5	20.7	2.8	23.1	89.3
GSC 98630	16.0	16.0	8.0	50	3.3	20.6	4.4	27.5	75
GSC 98633	14.8	14.8	7.6	51.4	2.7	18.3	3.5	23.6	77.2
GSC 95575	c17	12.5	6.0	48	2.5	20	3.6	29	69.4
MEAN				50.1		20.6		25.4	82.2
ST. DEV.				2.6		1.9		2.7	12.3

and Rivas, 1982; Dommergues, Ferretti, Géczy and Mouterde, 1983). *Leptonotoceras* is a morphologically similar form sometimes included as a subgenus of *Gemmellaroceras.* It is more cosmopolitan in its distribution and restricted to the uppermost Sinemurian. Hillebrandt (1973a, 1981) reports *Gemmellaroceras* from the Lower Pliensbachian of Argentina, although it is not figured.

Gemmellaroceras aenigmaticum
(Gemmellaro, 1884)
Plate 6, figures 19–23; Text-figure 26e

Aegoceras aenigmaticum Gemmellaro, 1884, p. 189, pl. 3, figs. 12, 14 and 15; pl. 4, fig. 10; pl. 7, fig. 20.
Gemmellaroceras aenigmaticum (Gemmellaro). Braga, Comas-Rengifo, Goy, and Rivas, 1982, pl. 1, figs. 2, 3.
Gemmellaroceras aff. *aenigmaticum* (Gemmellaro). Dommergues, Ferretti, Géczy, and Mouterde, 1983, p. 475, pl. 1, figs. 1–12.

Description.—The largest specimen available for study is 20 mm in diameter but most are between 10 and 15 mm in diameter. The shell is very evolute and slowly expanding with a rounded whorl section that becomes more compressed with growth. The rounded venter is featureless. The shell is generally smooth with coarse, simple ribs arising irregularly at larger diameters.

Type material.—Holotype: Gemmellaro, 1884, pl. 3, figs. 12, 14, 15 (Hyatt, 1900, p. 574).

Material.—Eighteen specimens preserved in sandstone and siltstone of the Rennell Junction Member.

Measurements.—See Table 15.

Discussion.—The Canadian material consists of individuals that are small compared to the Sicilian holotype which reaches a diameter of almost 30 mm. There is no evidence that the Canadian specimens are mature and some are completely septate so that this size discrepancy is not considered significant.

Occurrence.—This is a Tethyan species reported from the Iberian Peninsula (Dommergues *et al.,* 1983; Braga *et al.*, 1982), Morocco (Dubar and Mouterde, 1978), and Italy (Gemmellaro, 1884) where it is characteristic of the Jamesoni and Ibex zones.

Localities.—B04, ET1, E43, GT3.

Age.—Whiteavesi and lowest Freboldi zones (Early Pliensbachian).

Gemmellaroceras cf. alloplocum
(Gemmellaro, 1884)
Plate 10, figures 5, 6

cf. *Aegoceras alloplocum* Gemmellaro, 1884, p. 187, pl. 4, figs. 17–20; pl. 7, fig. 22.

Description.—Very evolute (U=c50), slowly expanding forms that reach shell diameters of 30 to 35 mm and bear weak, simple ribs that become slightly stronger with growth. The ribs, whose densities are typically 18 to 22 ribs per half whorl, project onto the venter which is angular but apparently does not bear a keel.

Material.—Approximately 25 poorly preserved molds in siltstone and rarely, fine sandstone mostly from the Ghost Creek Formation with one occurrence in the basal Fannin Formation.

Discussion.—As far as preservation permits comparison, these forms most closely resemble *Gemmellaroceras alloplocum* whose close affinity to early forms of *Tropidoceras* such as *T. erythraeum* has been noted by Braga and Rivas (1985).

Occurrence.—*G. alloplocum* in Sicily occurs in beds that correlate approximately with the Jamesoni and Ibex zones. This species may also be present in the Hall Formation of southern British Columbia as discussed under *Miltoceras* cf. *sellae.*

Localities.—E08, E13, E14, E16, E19, G01, G03, G04.

Age.—Characteristic of the Imlayi Zone with one occurrence in the basal Whiteavesi Zone (Early Pliensbachian).

Gemmellaroceras sp.
Plate 6, figures 12–14

Description.—Extremely evolute and slowly expanding form with a slightly wider than high whorl section. There is no keel. Ribs are densely spaced, simple and coarse; they begin to project but fade quickly at the ventro-lateral shoulder leaving the venter featureless.

Table 16.—Measurements of *Polymorphites confusus* (Quenstedt, 1856). All measurements are in mm.

specimen no.	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WW-WH*	*PR-HW*
GSC 98626	25.5	11.9	46.7	6.3	24.7	7.8	30.6	80.8	23
GSC 98595	17.1	8.0	46.8	5.7	33.3	6.4	37.4	89.1	17
GSC 98628	23.0	9.2	40	6.4	27.8	7.3	31.7	87.7	17
GSC 98627	21.6	10.3	47.7	5.6	25.9	6.1	28.2	91.8	21
MEAN			45.3		27.9		32	87.4	
ST. DEV.			3.6		3.8		3.9	4.7	

On two of the specimens (Plate 6, figs. 12 and 13) the ribbing fades and disappears.

Material.—Three specimens from the Rennell Junction Member.

Discussion.—The specimens are too small to make meaningful measurements and their small size makes them difficult to identify to the species level. They differ from other species of *Gemmellaroceras* by their very low expansion rate, their stout whorl section and their coarse ribs.

Locality.—FT1.

Age.—Associated with ammonites of the Freboldi Zone (Early Pliensbachian).

Genus **POLYMORPHITES** Haug, 1887

Type species.—*Ammonites polymorphus quadratus* Quenstedt 1845, pl. 4, fig. 9, by subsequent designation (Roman, 1938, p. 103).

Remarks.—Small, evolute forms with a subquadrate whorl section and simple ribs that are commonly tuberculate. Ventral features are disturbingly variable including plain, keeled, and keel-less with transverse ribbing.

Age and distribution.—*Polymorphites* is a widespread genus with most of its species occurring in northwest Europe. It is restricted to the Jamesoni Zone. The genus has been previously but only tentatively recognized in western North America and South America (Hillebrandt, 1987; Thomson and Smith, 1992).

Polymorphites confusus (Quenstedt, 1856)
Plate 6, figures 15–18; Text-figure 32c

Ammonites confusus Quenstedt, 1856, p. 127, pl. 15, figs. 8–10; 1885, p. 247, pl. 30, figs. 54–62.

Polymorphites confusus (Quenstedt). Schlegelmilch, 1976, p. 62, pl. 28, figs. 9, 10.

Polymorphites (Uptonia?) confusus (Quenstedt). Hoffmann, 1982, p. 189, pl. 19, figs. 1–5.

Description.—Evolute, slowly expanding forms with a compressed, subquadrate whorl section. The low umbilical wall rounds evenly into the gently convex flanks; the keel-less venter is gently arched but becomes flat with growth. No suture lines are visible so that the length of the body chamber is not known.

Ornamentation consists of dense, simple ribs that bear weak tubercles at the ventro-lateral shoulder. The ribs arise on the umbilical wall, trend rectiradiately to gently prorsiradiately across the flanks to the ventrolateral shoulder where they project weakly onto the venter and fade very rapidly.

Material.—Seven specimens and several whorl fragments preserved in limestone and one mold preserved in siltstone of the Ghost Creek Formation and Rennell Junction Member.

Measurements.—See Table 16.

Discussion.—These specimens differ from the inner whorls of *Dubariceras* and *Metaderoceras* with which they may be associated, in being more evolute and more slowly expanding, in having a less compressed whorl section and in having ribs that project onto the venter.

Occurrence.—This species is known from Germany (Hoffmann, 1982) and Portugal (Mouterde, 1967) where it occurs in the Jamesoni Zone.

Localities.—B04, E02, E03, E08, E17, G02, G03, G05, G09, H01.

Age.—Imlayi to lowest Freboldi Zone (Early Pliensbachian).

Subfamily **ACANTHOPLEUROCERATINAE**
Arkell, 1950

Genus **ACANTHOPLEUROCERAS** Hyatt, 1900

Type species.—*Ammonites valdani* d'Orbigny, 1844, pl. 42, by subsequent designation. Hyatt (1900, p. 578) designated *Ammonites natrix* Schlotheim, 1820, as the type species but he based this on Zieten's illustration (1830, pl. 4, fig. 5) of *Ammonites natrix,* the only representation of the species available at the time. As pointed out by Quenstedt (1849) and later Jaworski (1931), who was the first to figure the holotype, Schlotheim's species is in fact an echioceratid. *Acanthopleuroceras* was therefore based on a misidentified type species. Bremer (1965, p. 185) renamed *Ammonites natrix sensu* Zieten as *Acanthopleuroceras pseudonatrix,* and this was accepted as the type species by Frebold (1970, p. 439), although Bremer had pointed out its unsuitability in this respect. The type material is lost and there is some doubt as to the accuracy of Zieten's figure so that Getty (1970) finally proposed *Ammonites binotatus* Oppel, 1862 as the type species. Getty considered *Ammonites binotatus* as the new name for *Ammonites valdani* d'Orbigny, 1844, a homonym of *Ammonites ("Turrilites") valdani* d'Orbigny, 1842. D'Orbigny's 1844 species was upheld (ICZN Opinion

Table 17.—Measurements of *Acanthopleuroceras thomsoni,* new species. All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*PRHW*
GSC 98637	c37	27.6	12	43.5	8	29.0	8.6	31.2	93.0	19
		—	6	—	—	—	—	—	—	20
GSC 98639	—	—	11	—	6.3	—	7	—	90.0	19
GSC 98638	28.4	28.4	11.4	40.1	8.3	29.2	9.6	33.8	86.5	19
		—	7.2	—	—	—	—	—	—	19
GSC 98635	42	42	19.8	47.1	—	—	13.5	32.1	—	20
MEAN				43.6				32.4	89.8	
ST. DEV.				3.5				1.3	3.3	

996, 1973), however, and it now becomes the type species of *Acanthopleuroceras.*

Remarks.—The whorl section is quadrate to subquadrate and the venter bears a conspicuous blunt keel. Secondary ribs are rare but one or two rows of tubercles are common. The suture line has a trifid lateral lobe.

Age and distribution.—Cosmopolitan and restricted to the Ibex Zone and its correlatives.

Acanthopleuroceras thomsoni, new species

Plate 7, figures 1–5; Text-figure 32d,f

Paltechioceras cf. *P. harbledownense* (Crickmay). Imlay, 1981, p. 34, pl. 4, figs. 18–21 only.

Acanthopleuroceras aff. *stahli* (Oppel). Smith, Tipper, Taylor and Guex, 1988, Text-figure 1; Thomson and Smith, 1992, p. 18, pl. 5, figs. 1–4.

Description.—Evolute forms with an oval whorl section that becomes rectangular and compressed at umbilical diameters greater than approximately 10 mm. The flattened venter bears a low keel that is sometimes weakly sulcate. Ornamentation consists of densely spaced, rursiradiate ribs that swell or bear small rounded tubercles at their ventral ends. The nucleus is smooth but the ribbing, once established, maintains a density of approximately 19 or 20 ribs per half whorl throughout ontogeny. The suture line is not known.

Type material.—Holotype: GSC 9863 (Pl. 7, fig. 4). Paratypes: GSC 98635 (Pl. 7, fig. 1), GSC 98636 (Pl. 7, fig. 2), GSC 98637 (Pl. 7, fig. 3), GSC 98639 (Pl. 7, fig. 5).

Material.—Approximately 50 specimens in limestone, fine sandstone and siltstone of the Ghost Creek Formation and Rennell Junction Member.

Measurements.—See Table 17.

Derivation of name.—The species is named in honor of Mr. R. Thomson (Chevron Canada Ltd.) for his work on the Jurassic of northern British Columbia.

Discussion.—This form differs from *A. whiteavesi* with which it is commonly found and is closely related, by its denser, more rursiradiate ribbing, the presence of tubercles, and the weakly sulcate keel. It differs from *A. stahli* by its single rather than double row of tubercles. Two specimens identified as *Tropidoceras* sp. by Frebold (1970) are tentatively considered as variants of *A. thomsoni.* The first (Frebold, 1970, pl. 1, fig. 17) almost certainly belongs to *A. thomsoni* since it is identical to the holotype except for the ventral ends of the ribs which are not tuberculate or notably swollen. The second specimen (Frebold, 1970, pl. 2, fig. 16) differs from *A. thomsoni* by its more rectiradiate, more densely spaced ribs.

The inclusion of some specimens of *Paltechioceras* cf. *harbledownense* from southern Alaska identified by Imlay (1981) is based on examination of the material which shows the presence of ventral tubercles on the ribs; tubercles are unknown in the echioceratidae.

When preservation is poor, this form can superficially resemble species of *Arieticeras* seen higher in the section but the presence of tubercles on *Acanthopleuroceras thomsoni* serves as a readily distinguishable character.

Occurrence.—A species apparently endemic to the northeastern Pacific where it has been recorded from Alaska, British Columbia, Nevada and Oregon (Imlay, 1981; Smith, 1981; Thomson and Smith, 1992).

Localities.—A06, A08, A10, B04, E27, E33–37, E41, GT1, GT3, H08, H09, I01, I02, I16.

Age.—Whiteavesi Zone (Early Pliensbachian).

Acanthopleuroceras whiteavesi

Smith and Tipper, 1988

Plate 7, figures 6–10; Text-figures 26c, 32g-h

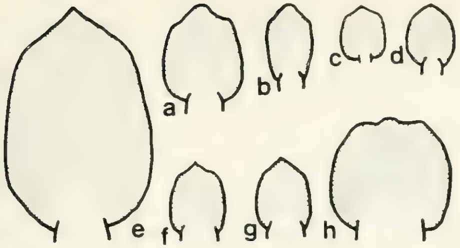
Tropidoceras actaeon (d'Orbigny). Frebold, 1970, p. 440, pl. 2, figs. 13–15.

Acanthopleuroceras whiteavesi Smith and Tipper *in* Smith, Tipper, Taylor and Guex, 1988, p. 1519, pl. 2, figs. 1–4.

Acanthopleuroceras cf. *whiteavesi* Smith and Tipper. Hillebrandt *in* Westermann, 1992, pl. 11, fig. 3a,b.

Description.—This species was erected using type material from the Queen Charlotte Islands and fully described by Smith *et al.* (1988) to which the reader is referred.

Type material.—Holotype: GSC 87790 (Smith *et al.,*



Text-figure 32.—Whorl shape cross-sections for species of the Polymorphitidae. Figures are natural size. a. *Tropidoceras* n. sp. (GSC 98648); b. *Tropidoceras actaeon* (D'Orbigny, 1844) (GSC 98645); c. *Polymorphites confusus* (Quenstedt, 1856) (GSC 98626); d,f. *Acanthopleuroceras thomsoni,* n.sp. (d. Holotype GSC 98638, f. Paratype GSC 98637); e. *Tropidoceras masseanum rotunda* (Futterer, 1893) (Holotype GSC 95573); g-h. *Acanthopleuroceras whiteavesi* Smith and Tipper, 1988 (g. GSC 98653, h. Holotype GSC 87790).

1988, pl. 2, figs. 1, 2; refigured herein, Pl. 7, fig. 7). Paratype: GSC 87791 (Smith *et al.,* pl. 2, figs. 3, 4; refigured herein, Pl. 7, fig. 6).

Material.—Forty-three specimens preserved in limestone, sandstone, and, rarely, in siltstone of the Sandilands and Ghost Creek formations and the Rennell Junction Member.

Occurrence.—This species is the zonal index for the Whiteavesi Zone to which it is restricted. Apart from the Queen Charlotte Islands, the species is also known from the Hurwal and Keller Creek formations of Oregon, information inadvertently omitted from the original species description by Smith and Tipper (*in* Smith *et al.*, 1988, p. 1521).

Localities.—A01, A02, A06, B03, C02, D02, D07, D11, ET1, E27, E34, E35, G04, I16.

Age.—Whiteavesi Zone (Early Pliensbachian).

Genus **TROPIDOCERAS** Hyatt, 1867

Type species.—*Ammonites masseanum* d'Orbigny, 1844, pl. 58, by subsequent designation (Haug, 1885, p. 606).

Remarks.—Fairly evolute forms with a compressed whorl section bearing a sharp keel. Ribbing is often weak and sometimes divided into primaries and secondaries. Species are non-tuberculate or weakly bituberculate. The suture line is complex with a bifid lateral lobe. Most workers have concluded that *Tropidoceras* and *Acanthopleuroceras* are closely related (*e.g.,* Dommergues and Mouterde, 1978, but see Wiedenmayer, 1977) and some species such as *A. stahli* and *A. rursicosta* are difficult to assign to either genus with confidence. In addition, Braga and Rivas (1985) have pointed out that *Tropidoceras* lies morphologically and chronologically between the genera *Gemmellaroceras* and *Acanthopleuroceras.*

Age and distribution.—Widely distributed but most diverse in the Jamesoni and Ibex zones of the Mediterranean region (Schlatter, 1980; Braga and Rivas, 1985).

Tropidoceras actaeon (d'Orbigny, 1844)
Plate 8, figures 1–3, 6; Text-figure 32b

Ammonites actaeon d'Orbigny, 1844, p. 232, pl. 61, figs. 1–3.

Cycloceras actaeon Futterer, 1893, p. 329, pl. 12, figs. 1, 2.

Tropidoceras aff. *actaeon* (d'Orbigny). Spath, 1928, p. 228, pl. 16, fig. 7.

Tropidoceras actaeon (d'Orbigny). Spath, 1928, p. 229, pl. 17, fig. 9; Wiedenmayer, 1980, p. 175, fig. 54a–c; Imlay, 1981, p. 37, pl. 8, figs. 1–9; Meister, 1986, p. 53, pl. 8, fig. 5.

Tropidoceras actaeon orientale (d'Orbigny). Bremer, 1965, p. 189, pl. 16, fig. 9; Text-figure 3.

non *Tropidoceras actaeon* (d'Orbigny). Frebold, 1970, p. 440, pl. 2, figs. 13–15 (=*Acanthopleuroceras whiteavesi*).

Acanthopleuroceras actaeon (d'Orbigny). Mouterde and Dommergues, 1978, fig. 25; Dommergues and Mouterde, 1978, fig. 2, no. 6; pl. 3, figs. 6–8.

Acanthopleuroceras cf. *actaeon* (d'Orbigny). Dommergues and Mouterde, 1981, p. 85, pl. 1, fig. 17.

Description.—Moderately evolute form with an oval whorl section. On early whorls the venter is angular but not sharp and there is an indistinct keel. On outer whorls, no keel is evident. Ribs are simple, not densely spaced and trend rectiradiately to gently rursiradiately towards the venter where they project weakly before quickly fading.

Type material.—Holotype: *Ammonites actaeon* d'Orbigny, 1844, pl. 61, figs. 1–3. Neotype designated and figured by Wiedenmayer, 1980, p. 175, Text-figure 54a–c.

Material.—Approximately 50 specimens mostly preserved as molds in siltstone and mudstone with a few in calcareous sandstone. Collected from the Ghost Creek Formation and Rennell Junction Member.

Measurements.—See Table 18.

Discussion.—This species is placed in *Tropidoceras* rather than *Acanthopleuroceras* because of its whorl shape and ventral features. A lectotype, which is slightly more evolute and more densely ribbed than the holotype of d'Orbigny (1844), is figured by Wiedenmayer (1980). The North American material most closely resembles d'Orbigny's holotype.

Occurrence.—*T. actaeon* is a widely distributed species characteristic of the Ibex Zone and its equivalents in Europe. In North America it is known from British Columbia and Alaska.

Localities.—A04, A05, DO3, DO5–08, D10–12, ET2, E10, E13, E18, E20–27, E30, E34, F01, GT1, GO5, G09, HO2, HO3, HO5-O7, IO2.

Table 18.—Measurements of *Tropidoceras actaeon* (d'Orbigny, 1844). All measurements are in mm.

specimen no.	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*PRHW*
GSC 98645	48	21	44	c11.5	c0.24	15.2	31.7	c75.7	17
	—	10	—	—	—	—	—	—	15
	—	4.1	—	—	—	—	—	—	15

Age.—Upper Imlayi and Whiteavesi zones (Early Pliensbachian).

Tropidoceras cf. **erythraeum** (Gemmellaro, 1884)
Plate 10, figures 4, 7

cf. *Harpoceras erythraeum* Gemmellaro, 1884, p. 40, pl. 5, figs. 10–16.

cf. *Tropidoceras erythraeum* (Gemmellaro). Levi, 1896, p. 274, pl. 8, fig. 10; Fucini, 1896, p. 248, pl. 25, fig. 22; Bremer, 1965, p. 187, text-fig. 2c; Braga and Rivas, 1985, p. 576, pl. 1, figs. 1, 2.

Tropidoceras aff. *erythraeum* (Gemmellaro). Smith, Tipper, Taylor and Guex, 1988, pl. 1, fig. 9.

Description.—An evolute form that becomes more involute with growth. The whorl section was probably compressed and a sharp keel is evident. Early whorls are smooth or very weakly ornamented. At umbilical diameters of between 1 and 2 cm, broad, distantly spaced ribs are evident on the lower part of the flank.

Type material.—Lectotype: Gemmellaro, 1884, pl. 5, figs. 10, 11 designated by Bremer (1965, p. 187).

Material.—Twenty-five poorly preserved molds in siltstone and shale of the Ghost Creek Formation.

Occurrence.—*T. erythraeum* is the earliest occurring species of *Tropidoceras* (Jamesoni Zone). The species is circum-Mediterranean in its distribution (Turkey, Italy, Spain) and its affinities have been discussed by Braga and Rivas (1985).

Localities.—A02, EO1, EO5, EO7, E10, GO1–3, IO8–11.

Age.—Imlayi Zone (Early Pliensbachian).

Tropidoceras flandrini flandrini
(Dumortier, 1869)
Plate 9, figures 1, 2, 4

Ammonites flandrini Dumortier, 1869, p. 72, pl. 14, figs. 1, 2.

Tropidoceras flandrini (Dumortier). Fucini, 1900, p. 24, pl. 5, fig. 2; Braga and Rivas, 1985, p. 572, pl. 1, fig. 3, pl. 2, fig. 1; Meister, 1986, p. 43, pl. 8, fig. 6; Smith, Tipper, Taylor and Guex, 1988, pl. 2, fig. 6.

Tropidoceras cf. *flandrini* (Dumortier). Géczy, 1976, p. 92, pl. 17, figs. 8, 9.

Tropidoceras flandrini densicosta (Dumortier). Wiedenmayer, 1977, p. 64, pl. 14, figs. 1, 2.

Tropidoceras flandrini cf. *obtusum* (Futterer). Hillebrandt, 1987, pl. 3, figs. 4, 5.

Description.—Evolute form bearing weak ribs that become stronger, more densely spaced and bituberculate with growth. Primary ribs are fine and bear numerous fine secondary ribs that project onto the venter where a low keel is evident.

Type material.—Holotype: Dumortier, 1869, pl. 14, figs. 1, 2.

Material.—Nine specimens in dark siltstone and fine sandstone of the Ghost Creek Formation.

Measurements.—See Table 19.

Discussion.—There are three subspecies of *T. flandrini* recognized by various workers, the other two being *T. f. densicosta* (Futterer, 1893) and *T. f. obtusa* (Futterer, 1893). *T. f. densicosta* is compressed with densely spaced, weak costation; *T. f. obtusa* has a subquadrate whorl section with strong, coarser, slightly less dense costation and *T. f. flandrini* sits between these extremes. These subspecies probably reflect covariation within a single species although *T. f. densicosta* has not been recognized in the Queen Charlotte Islands collections to date.

Occurrence.—This form is common in the Mediterranean region of the Tethyan Realm as far north as southern France and southern Germany where it appears in the Jamesoni Zone and ranges into the Ibex Zone (Schlatter, 1980; Dommergues, Mouterde, and Phelps, 1984). In South America it is known from the "*Tropidoceras*" zone in Argentina (Hillebrandt, 1987).

Localities.—A08, DO4, DO7, GO3, GO4, HO4, IO8.

Age.—Imlayi and lower Whiteavesi zones (Early Pliensbachian).

Tropidoceras flandrini obtusa
(Futterer, 1893)
Plate 8, figure 5; Plate 9, figures 3, 5

Cycloceras flandrini Dumortier var. *obtusa* Futterer, 1893, p. 334, pl. 13, fig. 1.

Tropidoceras cf. *flandrini* (Dumortier). Thomson and Smith, 1992, p. 19, pl. 5, fig. 5.

Description.—Evolute form that expands fairly rapidly compared to many other species of *Tropidoceras.*

Table 19.—Measurements of *Tropidoceras flandrini flandrini* (Dumortier, 1869). All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WH*	*WHD*	*PRHW*
GSC 87793	c95	80	34	42.5	27	33.8	c18
GSC 95574	64	64	27	42.2	21	32.8	18
		—	16	—	—	—	11

Table 20.—Measurements of *Tropidoceras masseanum rotunda* (Futterer, 1893). All measurements are in mm.

specimen no.	*DM-AX*	*D*	*UD*	*U*	*WW*	*WH*	*WHD*	*WW-WH*	*PR-HW*
GSC 95573	c95	72	26.5	36.8	—	c27	37.5	—	12
		—	c20	—	14	20.4	—	68.6	11

Whorls are compressed with a low keel and, for much of ontogeny, bear only coarse, widely spaced primary ribs that are rursiradiate in trend. At umbilical diameters of approximately 35 mm, the primary ribs become strongly bituberculate with an average of four secondaries arising per primary. The secondary ribs project onto the venter.

Type material.—Holotype: Futterer, 1893, pl. 13, fig. 1.

Material.—Seven specimens in dark siltstone, only moderately well preserved. Collected from the Ghost Creek Formation.

Discussion.—This variant differs from *T. flandrini flandrini* recognized herein, by its much sparser and coarser ribbing.

Occurrence.—This form is known from the Ibex Zone of southern Germany (Schlatter, 1980) and the Whiteavesi Zone of northern British Columbia (Thomson and Smith, 1992).

Localities.—DO1, DO8, I08.

Age.—Imlayi and Whiteavesi zones (Early Pliensbachian).

Tropidoceras masseanum rotunda
(Futterer, 1893)
Plate 10, figures 1, 2; Text-figure 32c

Cycloceras masseanum d'Orbigny var. *rotunda* Futterer, 1893, p. 330, pl. 12, figs. 3, 4.

Tropidoceras masseanum (d'Orbigny) *rotunda* (Futterer). Schlatter, 1980, p. 138, pl. 19, fig. 4; pl. 20, figs. 1, 2; fig. 11, g–i.

Tropidoceras masseanum rotunda (Futterer). Meister, 1986, p. 45, pl. 6, fig. 6; pl. 7, fig. 1.

Description.—Large specimens (Pl. 10, fig. 1 is completely septate) that are moderately evolute and have a compressed whorl section bearing a low keel. The ribs are robust and tubercles are not present. The ribbing is rectiradiate to gently rursiradiate and projects onto the venter. The umbilical wall is high and rounded, the flanks weakly convex.

Type material.—Holotype: Futterer, 1893, pl. 12, figs. 3, 4.

Material.—Twenty-five specimens preserved in siltstone and calcareous concretions; mostly fragments and external molds. Collected from the Sandilands and Ghost Creek formations and Rennell Junction Member.

Table 21.—Measurements of *Tropidoceras* aff. *rursicosta* (Buckman, 1918). All measurements are in mm.

specimen no.	*D*	*UD*	*U*	*WH*	*WHD*	*PRHW*
GSC 98650	80	40	50	24	30	c14

Measurements.—See Table 20.

Discussion.—This form differs from *Tropidoceras masseanum masseanum* (d'Orbigny, 1884) by its stouter whorl section, coarser ribbing and slightly more evolute coiling.

Occurrence.—*T. m. masseanum* is widely distributed and particularly common in the Tethyan area of southern Europe. *T. masseanum rotunda* has been reported from southern Germany and southern France where it is characteristic of the lower Ibex Zone.

Localities.—A01, C02, D06–08, D10, D11, ET1, ET2, E18, E21, E23, E25, E27–31, E37, E39, GT3, G06, I02.

Age.—Whiteavesi Zone (Early Pliensbachian).

Tropidoceras aff. **rursicosta** (Buckman, 1918)
Plate 8, figure 7

aff. *Ammonites valdani* d'Orbigny. Quenstedt, 1885, p. 278, pl. 35, fig. 4.

aff. *Acanthopleuroceras rursicosta* Buckman, 1918, p. 286, pl. 26, fig. 4.

aff. *Tropidoceras rursicosta* (Buckman). Schlatter, 1980, p. 147, pl. 22, fig. 4.

Description.—Evolute, slowly expanding forms, the largest specimen of which is figured. No sutures are visible so that the length of the body chamber is unknown. The whorl section is probably subquadrate bearing a low, blunt keel. The umbilical wall is low and rounds evenly into the gently convex flanks.

There is no ribbing on the inner whorls until an umbilical diameter of 8 to 10 mm at which point broad, weak primary ribs arise that are rursiradiate and commonly swollen near the umbilicus. On larger whorls, the strength of the ribbing increases and three or four secondary ribs per primary rib project onto the venter.

Type material.—Holotype for *Tropidoceras rursicosta*: Buckman, 1918, pl. 26, fig. 4.

Material.—Four specimens, poorly preserved in mudstone and siltstone of the Ghost Creek Formation.

Measurements.—See Table 21.

Discussion.—This material represents a new species related to the large form *Tropidoceras rursicosta* which is characterized by its strongly rursiradiate, commonly tuberculate primaries and projected secondary ribs. The state of preservation of the material, however, does not warrant the establishment of a new species name.

A large specimen held in the collections of the Natural History Museum, London (number C22346) was referred to *T. rursicosta* by Spath (1922, p. 124). It was labelled as originating from Vancouver Island (Hector collection) and included in a collection of Cretaceous age. Spath (1922) believed the specimen misplaced and suggested that it originated, like Buckman's specimen of *Acanthopleuroceras rursicosta,* from the Carixian (Lower Pliensbachian) of Gloucestershire. The possibility of it originating from the Insular Belt of British Columbia (and perhaps representing the species *T.* aff. *rursicostata* described here), however, cannot be discounted. Jurassic and Cretaceous faunas were commonly confused by early workers in this area (see Whiteaves, 1884).

Occurrence.—*T. rursicosta* is known from the Ibex Zone of Britain and the Valdani subzone of the Ibex Zone in Germany.

Localities.—E01, I08, I11, I13.

Age.—Imlayi Zone (Early Pliensbachian).

Tropidoceras new species 1

Plate 8, figure 4; Text-figure 32a

Description.—Midvolute form with a compressed whorl section. The umbilical wall is fairly high and steeply inclined, the venter angular bearing a low keel. Ribbing is coarse and rursiradiate with rounded tubercles at the ventro-lateral shoulder. The ribs weaken dramatically at the ventro-lateral shoulder and can barely be seen projecting onto the venter. No sutures are visible.

Material.—One moderately well preserved, slightly distorted internal mold and two whorl fragments preserved in sandstone of the Rennell Junction Member.

Discussion.—A somewhat similar specimen is known from southern Germany (Schlatter, 1980, p. 148, pl. 22, fig. 5) but it does not bear well marked tubercles and its inner whorls are not preserved making comparisons difficult. More material is needed before this probable new species can be properly documented.

Occurrence.—This form is only known from the Queen Charlotte Islands.

Localities.—E34, I02.

Age.—Whiteavesi Zone (Early Pliensbachian).

Tropidoceras new species 2

Plate 10, figure 3

Description.—Because of the incomplete nature of this material it is not possible to make measurements but the shell was moderately evolute with a compressed whorl section (WWWH=c63) bearing a weak keel. The umbilical wall is steep but rounds rapidly into the flattened flanks. The ribs are flexuous and strongly rursiradiate. A few ribs swell at their ventral ends and all the ribs fade as they project onto the venter where very weak striations can be seen.

Material.—Two fragments of specimens in calcareous sandstone of the Ghost Creek Formation.

Discussion.—The volution and whorl shape of these specimens are reminiscent of more finely ribbed forms of *T. masseanum* but the rursiradiate trend of the ribbing sets this material apart. It cannot be established as a new species, however, until more material is collected.

Localities.—ET1, E14.

Age.—Imlayi Zone (Early Pliensbachian).

Tropidoceras species 1

Plate 11, figures 1–3

Description.—Very evolute, slowly expanding forms with weak simple ribs that become stronger at umbilical diameters of 15 to 20 mm. A keel is evident on some of the fragments.

Material.—Nine poorly preserved molds in siltstone of the Ghost Creek Formation and Rennell Junction Member.

Discussion.—The volution and expansion rate of this form are reminiscent of those seen in *Gemmellaroceras* although the presence of a keel and, to a lesser extent, the large size of the specimens leave no doubt that it should be assigned to *Tropidoceras.* Better preserved material must be collected before a confident identification can be made.

Localities.—DO1, E18, E20, GO1, I04, I08, I11.

Age.—Imlayi and Whiteavesi zones.

Family **PHRICODOCERATIDAE** Spath, 1938

Genus **PHRICODOCERAS** Hyatt, 1900

Hemiparinodiceras Géczy, 1959, p. 143.

Type species.—*Ammonites taylori* Sowerby, 1826 (pl. 514, figs. 1, 2), by original designation (Hyatt, 1900, p. 587).

Remarks.—Early ontogenetic stages have a rounded or depressed whorl section, are strongly ribbed and bear marked lateral and paired ventral tubercles. Outer whorls are compressed with weak or obsolete ornamentation.

Age and distribution.—*Phricodoceras* is known from the Jamesoni Zone of the Northwest European Province where the rare *P. taylori* is a subzonal index (Dean *et al.*, 1961). During the course of the Pliensbachian, the genus became widely distributed, from the Mediterranean region to as far east as Roti in Indonesia (Krumbeck, 1922). Outside Northwest Europe the genus is much longer ranging (Géczy, 1976; Fantini Sestini, 1978; Dubar and Mouterde, 1978; Bremer, 1965; Dommergues and Meister, 1990) particularly in Italy where it ranges from the Raricostatum to the Margaritatus zone. The genus is not, as yet, recorded from

South America but it is previously recorded from cratonal North America by Frebold (1970).

Phricodoceras cf. **taylori**
(J. de C. Sowerby, 1826)
Plate 15, figure 2

cf. *Ammonites taylori* J. de C. Sowerby, 1826, p. 23, pl. 514, fig. 1; d'Orbigny, 1844, p. 323, pl. 103, figs. 3, 4; Quenstedt, 1856, p. 125, pl. 16, fig. 8; Hauer, 1861, p. 413, pl. 1, figs. 21–22.
cf. *Ammonites lamellosus* d'Orbigny, 1844, p. 283, pl. 84, figs. 1, 2.
cf. *Aegoceras taylori* (J. de C. Sowerby). Wright, 1880, p. 348, pl. 31, figs. 5–7; Bettoni, 1900, p. 78, pl. 8, figs. 18, 19.
cf. *Phricodoceras taylori* (J. de C. Sowerby). Del Campana, 1900, p. 587, pl. 5, figs. 45–47; Bremer, 1965, p. 175; Dommergues, 1978, p. 41, figs. 1–3.
cf. *Phricodoceras lamellosum* (d'Orbigny). Buckman, 1920, pl. 149A–D.
Phricodoceras cf. *taylori* (J. de C. Sowerby). Frebold, 1970, pl. 2, figs. 11, 12; Smith, Tipper, Taylor and Guex, 1988, pl. 1, fig. 10.
Phricodoceras cf. *lamellosum* (d'Orbigny). Dubar and Mouterde, 1978, p. 51, pl. 3, fig. 3.
Phricodoceras aff. *taylori* (J. de C. Sowerby). Dommergues and Meister, 1990, p. 299, pl. 2, fig. 3.

Description.—This specimen had an estimated diameter of 40 mm and was midvolute with U at approximately 35–40 mm. The umbilical wall rounds evenly into the rounded flanks. Ribbing is fairly dense (PRHW=13 at UD=15 mm). The ribs are simple, gently prorsiradiate and sharper on the inner whorls. Two rows of tubercles are present, one on the upper third of the flank, the other on the lateral part of the venter. The venter itself is not visible.

Type material.—Holotype: J. de C. Sowerby, 1826, pl. 514, fig. 1.

Material.—One moderately well preserved external mold in siltstone of the Ghost Creek Formation.

Discussion.—As far as preservation permits comparison, this specimen is similar to *P. lamellosum* which is common in circum-Mediterranean countries. This species has been synonymized with *P. taylori* by Bremer (1965), Wiedenmayer (1977), and Dommergues (1978). Dommergues considers the two species to be sexual dimorphs.

Occurrence.—*P. taylori* is cosmopolitan and characteristic of the Raricostatum in the Sinemurian to as high as the Ibex zone in the Pliensbachian (Dommergues and Meister, 1990; Fantini Sestini, 1978).

Locality.—I08.

Age.—Imlayi Zone (Early Pliensbachian).

Family **EODEROCERATIDAE** Spath, 1929

Genus **PSEUDOSKIRROCERAS**
Wiedenmayer, 1980

Type species.—*Coeloceras mastodon* Fucini, 1935, p. 166, pl. 40, figs. 3, 4, by original designation (Wiedenmayer, 1980, p. 172).

Remarks.—Evolute, slowly expanding forms that can reach large shell diameters. The whorl section is compressed elliptical to rounded, and a row of tubercles is present, usually in the middle of the flank. Uniform secondary ribbing bifurcates from the tubercles and is sometimes accompanied by intercalated ribs. Wiedenmayer (1980) has noted that this genus which, as the name indicates, is a homeomorph of the Bajocian *Skirroceras,* is closely related to *Miltoceras.*

Age and distribution.—A Tethyan genus that Wiedenmayer (1980) states is characteristic of the Davoei and Margaritatus zones in Europe. It also occurs in the Upper Sinemurian or basal Pliensbachian of Chile (Hillebrandt, 1981) and the lowest Pliensbachian of North America (Smith *et al.*, 1988).

Pseudoskirroceras imlayi Smith and Tipper, 1988
Plate 13, figures 1–4; Plate 14, figures 1–4;
Plate 15, figure 1

Description.—Large, evolute forms with a slightly compressed whorl section and a gently rounded venter. Primary ribs are strong and prorsiradiate, bearing tubercles just above the middle of the flank. Weaker secondary ribs arise in pairs or threes from the tubercles; some intercalated ribs are present. Within the sample there is some variability shown in the strength of the ornamentation but at shell diameters of approximately 100 mm, ribbing weakens and the tubercles fade or disappear for approximately one half whorl followed by two or three coarse ribs (Pl. 13, fig. 2; Pl. 14, fig. 4).

Type material.—*Pseudoskirroceras imlayi* Smith and Tipper *in* Smith *et al.*, 1988, p. 1519, pl. 1, figs. 1–5; Holotype: GSC 87783; Paratypes: GSC 87784, 87785.

Material.—Approximately 135 molds and fragments preserved in mudstone and siltstone of the Ghost Creek Formation.

Discussion.—A full discussion of this species was given by Smith and Tipper (*in* Smith *et al.*, 1988). This species was included in *Pseudoskirroceras* rather than the closely related *Miltoceras* on grounds of: (i) its evolute, slowly expanding shell bearing regularly spaced ribs and tubercles, and (ii) its stratigraphic position which falls within the range of *Pseudoskirroceras* as known from elsewhere in the world. It should be noted, however, that the occurrence of *Pseudoskirroceras* and *Miltoceras* low in the Pliensbachian appears to be characteristic of the Americas. The ranges of the two genera in the Mediterranean area, where they are uncommon, overlap at a higher stratigraphic level within the Pliensbachian (Davoei Zone). Further work is required to finely document this difference and to explore its phylogenetic and biogeographic implications.

Occurrence.—This species is characteristic of the

Imlayi Zone of western North America (Smith *et al.*, 1988).

Localities.—BT1, B01, B02, C01, ET1, E04, E07, E09, E16, G01–03, I08–11.

Age.—Imlayi Zone (Early Pliensbachian).

Genus **MILTOCERAS** Wiedenmayer, 1980

Type species.—*Aegoceras sellae* Gemmellaro, 1884, p. 179, pl. 3, figs. 1–5 by original designation (Wiedenmayer, 1980, p. 172).

Remarks.—*Miltoceras* was created as a subgenus of *Apoderoceras* by Wiedenmayer (1980) and elevated to generic status by Hillebrandt (1981). It is characterized by coronate early whorls that quickly become compressed with subparallel flanks and an arched venter. The ribbing, which is often irregular, is characterized by dense prorsiradiate primary ribs with secondary ribs arising from tubercles on the upper half of the flank. The genus is similar to *Pseudoskirroceras* which differs by being more evolute, more slowly expanding and having more regular ribbing.

Age and distribution.—A Tethyan genus ranging from the Jamesoni to the Davoei zones (Wiedenmayer, 1980). In Chile and Argentina it is known from lowest Pliensbachian rocks (Riccardi, 1984; Hillebrandt, 1987, 1990b) and in rocks of the same age in northern British Columbia (Thomson and Smith, 1992).

Miltoceras aff. **sellae** (Gemmellaro, 1884)
Plate 11, figures 4–6

aff. *Aegoceras sellae* Gemmellaro, 1884, p. 179, pl. 3, figs. 1–5.
non *Coeloceras Sellae* (Gemmellaro). Monestier, 1934, p. 101, pl. 4, figs. 6, 7, 19, 20.
Apoderoceras (Miltoceras) cf. *sellae* (Gemmellaro). Hillebrandt, 1987, pl. 1, figs. 12–14; Hillebrandt *in* Westermann, 1992, pl. 11, fig. 1.

Description.—Moderately evolute form with a compressed whorl section and an arched, keel-less venter. The prorsiradiate primary ribs are gently flexuous and bear, sometimes at irregular intervals, small tubercles a little over half way to two thirds of the way up the flank. From the row of tubercles, two or three secondaries arise per primary mostly by intercalation, and flex forward onto the venter. Ribs become coarser and less densely spaced with growth. No septal suture lines can be seen and the material is too poorly preserved to make meaningful measurements.

Type material.—Lectotype of *Miltoceras sellae*: Gemmellaro, 1884, pl. 3, figs. 1–2 (designated herein).

Material.—Seventeen poorly preserved specimens in siltstone of the Ghost Creek Formation.

Discussion.—As far as preservation permits comparison, this material is identical to material from Chile described by Hillebrandt (1981, 1987) as *Apoderoceras (Miltoceras)* cf. *sellae*. It differs from this species mainly in its less regular tuberculation.

Occurrence.—In the Mediterranean area, this species and its varieties (Wiedenmayer, 1980) occur in beds that correlate approximately with the Jamesoni and Ibex zones (Gemmellaro, 1884; Rosenberg, 1909; Fucini, 1935; Du Dresnay, 1963). In South America, it occurs in the zone of "*Apoderoceras* and *Eoderoceras*" which marks the base of the Pliensbachian (Hillebrandt, 1987). This species might also be present in the Hall Formation of the Rossland area, southern British Columbia, amongst a poorly preserved fauna initially thought to be post-middle Bajocian in age (Frebold and Little, 1962) but subsequently assigned to the Pliensbachian by Tipper (1984). Amongst the forms initially assigned in that publication to *Perisphinctes?* appear to be *Miltoceras* cf. *sellae* (Frebold and Little, 1962, pl. 4, figs. 1, 3 and 4); *Metaderoceras* sp. (Frebold and Little, 1962, pl. 4, fig. 2); and *Gemmellaroceras* cf. *alloplocum* (Frebold and Little, 1962, pl. 4, fig. 5).

Localities.—BT1, CT1, ET1, E09, E11–14, G01-G03.

Age.—Imlayi Zone (Early Pliensbachian).

Genus **DUBARICERAS**
Dommergues, Mouterde, and Rivas, 1984

Type species.—*Dubariceras dubari* Dommergues, Mouterde, and Rivas (1984, p. 382, pl. 1).

Remarks.—The characteristics of this genus and the taxonomic problems resulting from its convergence with certain polymorphitids have been discussed by Dommergues *et al.* (1984) and Thomson and Smith (1992). *Dubariceras* is thought to have evolved from *Metaderoceras.*

Age and distribution.—*Dubariceras* is characteristic of the western Mediterranean and the eastern Pacific. In Europe it is characteristic of beds correlative with the Ibex and Davoei zones; in North America it occurs in the Whiteavesi and Freboldi zones.

Dubariceras freboldi
Dommergues, Mouterde, and Rivas, 1984
Plate 16, figures 1, 2; Text-figure 33e

Uptonia dayiceroides Mouterde. Frebold, 1970, p. 438, pl. 1, fig. 9.
Uptonia cf. *U. dayiceroides* Mouterde. Imlay, 1981, p. 36, pl. 9, figs. 1–4, 8, 12–16.
Uptonia cf. *U. angusta* (Oppel). Hillebrandt, 1981, p. 509, pl. 5, fig. 3.
Dayiceras dayiceroides (Mouterde). Smith, 1983, p. 86, fig. 2a–c.
Dubariceras freboldi Dommergues, Mouterde, and Rivas, 1984, fig. 3–A3; Smith, Tipper, Taylor and Guex, 1988, pl. 3, figs. 1–3; Thomson and Smith, 1992, p. 27, pl. 11, figs. 1–7.
Dayiceras? sp. Hillebrandt, 1987, pl. 2, figs. 11, 12.
Dubariceras cf. *freboldi* Dommergues, Mouterde, and Rivas. Hillebrandt, 1990a, fig. 4.10, ?4.11.

Description.—Evolute with a compressed whorl section and a flat to gently arched venter that has no keel. The umbilical wall is low and steep, the umbilical shoulder abruptly rounded, the flanks flat and the ventro-lateral shoulder abruptly rounded.

Ribs are densely spaced, rursiradiate on the umbilical wall, and rectiradiate to gently prorsiradiate on the flanks. Ribs terminate at the ventro-lateral shoulder with small, elongate tubercles.

Type material.—Holotype: Frebold, 1970, pl. 1, fig. 9.

Material.—Approximately 190 specimens, many of them fragments, preserved in siltstone and calcareous sandstone. Primarily from the Rennell Junction Member of the Fannin Formation with some occurrences in the Fannin sandstone and rare occurrences in the Ghost Creek Formation.

Discussion.—Full descriptions and discussions of the taxonomic position of this widespread and biostratigraphically useful species have been published by Frebold (1970), Imlay (1981), Smith (1983), Thomson and Smith (1992), and Dommergues *et al.* (1984).

Occurrence.—*D. freboldi* is endemic to the eastern Pacific where it occurs from Argentina and Chile in the south (Hillebrandt, 1981, 1990) as far north as southern Alaska (Imlay, 1981). In South America the species occurs in the Meridianus Zone, in North America in the Freboldi Zone, intervals that correlate in part with the Ibex and Davoei zones of the Northwest European zonation. There is one locality in the Queen Charlotte Islands (F06) where the uppermost part of the range of *Dubariceras freboldi* overlaps with the lowermost part of the range of *Fanninoceras* sp. so that the two forms occur in the same bed. These genera are normally mutually exclusive and a total of only three such overlapping occurrences is known in North America (Smith *et al.*, 1988). At all three of these localities (F06 in the Queen Charlotte Islands; the Taseko Lakes area, British Columbia; the Hurwal Formation, northwestern Oregon) *D. freboldi* is common or abundant and *Fanninoceras* (*F. fannini* and *F.* sp.) is rare and condensing cannot be ruled out. *D. freboldi* will only be considered as ranging into the Kunae Zone when there is significant stratigraphic overlap demonstrated between *D. freboldi* and an assemblage of *Fanninoceras* spp. and hildoceratids which normally characterizes the Kunae Zone.

Localities.—A12, A13, C03, D13–15, D18, ET1, ET3, E42–49, FT1, F05, F06, GT2, GT3, G10, G11, I01, I07, I15.

Age.—Freboldi Zone (Early Pliensbachian).

Dubariceras silviesi (Hertlein, 1925)
Plate 15, figures 3, 4

Uptonia silviesi Hertlein, 1925, p. 39, pl. 3, figs. 1, 2, 5.

Crucilobiceras cf. *C. submuticum* (Oppel). Imlay, 1981, p. 33, pl. 7, figs. 1–3.

Uptonia cf. *U. obsoleta* (Simpson). Hillebrandt, 1981, p. 509, pl. 5, figs. 1, 2, 5; 1987, pl. 2, figs. 1, 5.

Dubariceras silviesi (Hertlein). Smith, Tipper, Taylor and Guex, 1988, pl. 2, fig. 5; Smith and Tipper, 1988, pl. 1, fig. 6; Thomson and Smith, 1992, p. 29, pl. 10, fig. 2–5.

Dubariceras cf. *silviesi* (Hertlein). Hillebrandt, *in* Westermann, 1992, pl. 11, fig. 5.

Description.—Evolute shell with a subrectangular whorl section. Ribs are simple, straight to slightly sinuous, and prorsiradiate; they terminate at the ventro-lateral shoulder in prominent tubercles. The venter is featureless except at large shell diameters where the ribs project onto the venter to form chevrons.

Type material.—Holotype: Hertlein, 1925, pl. 3, figs. 1, 2, 5.

Material.—Seventeen specimens in siltstone and calcareous sandstone of the Ghost Creek Formation and Rennell Junction Member.

Discussion.—The holotype of this species from Oregon reaches a large size (whorl height in excess of 45 mm) and comparable sizes are reached in the Queen Charlotte Islands although only whorl fragments have been collected. The species appears to have affinities with both *Metaderoceras* and *Dubariceras* as discussed by Thomson and Smith (1992). It differs from *D. freboldi* which ranges stratigraphically higher, by its less dense ribbing.

Occurrence.—*D. silviesi* is restricted to the eastern Pacific where it is characteristic of the Whiteavesi and lower Freboldi zones in North America (Smith *et al.*, 1988) and the Meridianus Zone in South America (Hillebrandt, 1987, 1990) which correlate approximately with parts of the Ibex and Davoei zones of the European zonation.

Localities.—B04, E40, FT1, GT1, GT3, I01, I02, I07.

Age.—Whiteavesi and Freboldi zones (Early Pliensbachian).

Genus **METADEROCERAS** Spath, 1925

Type species.—*Ammonites muticus* d'Orbigny, 1844, p. 274, pl. 8, by original designation (Spath, 1925, p. 363).

Remarks.—Problems concerning the interpretation of this genus and the related genera *Crucilobiceras* and *Eoderoceras* are discussed by Thomson and Smith (1992).

Age and distribution.—*Metaderoceras* is widely distributed in the circum-Mediterranean region and the eastern Pacific. It occurs in the Jamesoni and Ibex zone equivalents in Europe and in the Imlayi to basal Kunae zone in western North America (Cólera *et al.*, 1978; Mouterde, 1970; Rivas, 1983; Smith *et al.*, 1988). In

South America it is reported from the Meridianus Zone which correlates in part with the Ibex and Davoei standard zones (Hillebrandt, 1981, 1987, 1990).

Metaderoceras evolutum is the earliest species of *Metaderoceras* in the Queen Charlotte Islands. In the Whiteavesi Zone it is joined by several other species of *Metaderoceras* which are generally more coarsely and more densely ribbed and which may have given rise to *Dubariceras.* This coarse ribbed group also includes the stout-whorled, strongly tuberculate *M. mouterdei* and related forms which are reminiscent of the circum-Mediterranean *M. venarense* group that Dommergues and Mouterde (1982) interpret to be the root-stock of the Dactylioceratidae in the Ibex Zone.

Metaderoceras evolutum (Fucini, 1924)
Plate 16, figures 3–5, 7; Plate 18, figure 1;
Text-figures 33b, 34a

Deroceras evolutum Fucini, 1924, p. 50, pl. 5, fig. 14.
Crucilobiceras aff. *evolutum* (Fucini). Du Dresnay, 1963, p. 147, pl. 2, figs. 2, 3.
Crucilobiceras pacificum Frebold, 1970, p. 435, pl. 1, figs. 4–8.
Crucilobiceras evolutum brutum Wiedenmayer, 1977, p. 59, pl. 13, figs. 1, 2.
Crucilobiceras evolutum evolutum (Fucini). Wiedenmayer, 1977, p. 59, pl. 13, fig. 3; 1980, p. 48, pl. 1, figs. 3, 4.
Metaderoceras evolutum (Fucini). Dubar and Mouterde, 1978, p. 44, pl. 2, fig. 1; Rivas, 1983, p. 395, pl. 1, figs. 1–8; Smith, Tipper, Taylor and Guex, 1988, pl. 1, fig. 11; Thomson and Smith, 1992, p. 22, pl. 9, figs. 5–6.
Metaderoceras evolutum brutum (Fucini). Colera, Rivas, Sequeiros and Valenzuela, 1978, p. 311, pl. 1, figs. 3, 4.
Crucilobiceras cf. *pacificum* Frebold. Imlay, 1981, p. 35, pl. 8, figs. 10–12, 15–17.

Description.—Shell evolute and slowly expanding. Whorl section usually compressed, subquadrate with a low umbilical wall, weakly convex flanks and a slightly convex or flat venter.

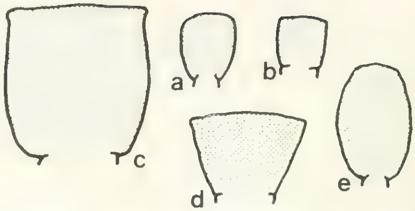
Ribs are rectiradiate to gently prorsiradiate and of low relief compared to other species of *Metaderoceras.* Two or three ribs merge into a large tubercle which is the base of a long spine. At large shell diameters (Pl. 18, fig. 1), ribs tend to become weakly rursiradate and terminate in individual spines rather than merging. Fine, irregular, radial lirae are evident throughout ontogeny.

Type material.—Holotype: Fucini, 1924, pl. 5, fig. 14.

Material.—Seventy-three specimens in siltstone and calcareous sandstone of the Ghost Creek Formation and Rennell Junction Member.

Discussion.—This variable species is discussed by Rivas (1983) and Thomson and Smith (1992).

Occurrence.—*M. evolutum* is common in the circum-Mediterranean region and western North America (Wiedenmayer, 1980; Rivas, 1983; Thomson and Smith, 1992).



Text-figure 33.—Whorl shape cross-sections for species of the Eoderoceratidae. Figures are natural size. a. *Metaderoceras talkeetnaense* Thomson and Smith, 1992 (GSC 98703); b. *Metaderoceras evolutum* (Fucini, 1921) (GSC 95576); c. *Metaderoceras* sp. (GSC 98702); d. *Metaderoceras*? aff. *mouterdei* (Frebold, 1970) (GSC 87797); e. *Dubariceras freboldi* (Dommergues et al., 1984) (GSC 98686).

Localities.—A03, A05, BT1, D03, D05, D07–D10, ET1, ET3, E06, E15, E25, E27, E30, GT1, G06, I08, I16.

Age.—Imlayi and Whiteavesi zones (Early Pliensbachian).

Metaderoceras mouterdei (Frebold, 1970)
Plate 19, figure 3

Crucilobiceras mouterdei Frebold, 1970, p. 437, pl. 1, fig. 2.
non *Metaderoceras mouterdei* (Frebold). Smith, Tipper, Taylor, and Guex, 1988, pl. 3, figs. 9, 10; Smith and Tipper, 1988, pl. 1, fig. 8 (see *M.*? aff. *mouterdei*).

Description.—An evolute, slowly expanding form with flanks that diverge weakly towards the slightly arched venter. Ribs are simple, gently prorsiradiate and terminate at the ventro-lateral shoulder in stout tubercles. The venter is unornamented. Rib frequency decreases with growth up to umbilical diameters of 25–30 mm.

Type material.—Holotype: Frebold, 1970, pl. 1, fig. 2; GSC 20337.

Material.—Eight specimens in sandstone of the Rennell Junction Member.

Discussion.—*M. mouterdei* is similar to *M. venarense* (Oppel), one of the highest ranging (Ibex Zone) species of *Metaderoceras* in southern Europe (Frebold, 1970; Dommergues and Mouterde, 1982). It differs, however, in its slightly narrower whorl section and in its ribbing which changes style and frequency during ontogeny.

Occurrence.—*M. mouterdei* is restricted to the Whiteavesi Zone of British Columbia. The similar *M. venarense* is known from the Ibex Zone of the Tethyan area particularly southern France and Portugal (Mouterde, 1970; Meister, 1986).

Localities.—ET1, E40, F02, GT3, G09, I02.

Age.—Whiteavesi Zone (Early Pliensbachian).

Metaderoceras? aff. mouterdei (Frebold, 1970)
Plate 16, figure 6; Plate 19, figure 4;
Text-figures 33d, 34b

aff. *Crucilobiceras mouterdei* Frebold, 1970, p. 437, pl. 1, fig. 2.
Apoderoceras cf. *A. subtriangulare* (Young and Bird). Imlay, 1981, p. 35, pl. 8, figs. 14, 18–23.
Metaderoceras mouterdei (Frebold). Smith, Tipper, Taylor, and Guex, 1988, pl. 3, figs. 9, 10; Smith and Tipper, 1988, pl. 1, fig. 8.
Metaderoceras cf. *M. mouterdei* (Frebold). Thomson and Smith, 1992, p. 23, pl. 9, figs. 1–4; pl. 10, fig. 1.

Description.—Evolute forms with whorl flanks diverging towards the venter which is characteristically broad. The innermost whorls are densely ribbed but the decrease in frequency and coarsening of the ribbing is typically underway at umbilical diameters less than 10 mm. The ribs strengthen ventrally and terminate in large tubercles which are the bases of robust spines. Ribs are rectiradiate to gently prorsiradiate and may be locally irregular or weakly sinuous at large shell diameters (Pl. 19, fig. 4).

Material.—Twelve specimens in sandstone and siltstone of the Fannin Formation.

Discussion.—This is the stratigraphically highest ranging, and amongst the most strongly ornamented species of *Metaderoceras* yet described in North America. We previously included this form in *M. mouterdei* with which it has morphological similarities (Smith *et al.*, 1988; Thomson and Smith, 1992). It is difficult, however, to demonstrate that *M. mouterdei* and *M.?* aff. *mouterdei* represent variants, particularly as there is a discrepancy in stratigraphic range. In fact the exceptionally broad, *Eoderoceras*-like venter of *M.?* aff. *mouterdei* makes it difficult to unequivocally accommodate this form in the genus *Metaderoceras*. *Eoderoceras*-like forms are known in the eastern Pacific but they characterize the lowest Pliensbachian (Hillebrandt, 1981, 1987).

Occurrence.—This form is apparently indigenous to North America where it characterizes the Whiteavesi to basal Kunae zones.

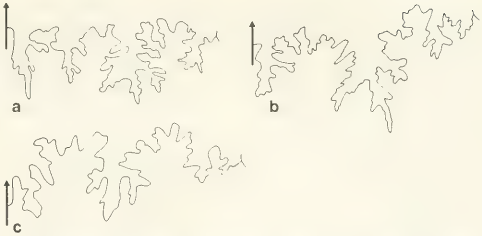
Localities.—C03, C05, ET3, E38.

Age.—Whiteavesi to Kunae Zone (Pliensbachian).

Metaderoceras talkeetnaense
Thomson and Smith, 1992
Plate 17, figures 2, 3; Text-figures 33a, 34c

Crucilobiceras cf. *C. muticum* (d'Orbigny). Imlay, 1981, p. 35, pl. 7, figs. 6–10, 12–15.
Uptonia cf. *ignota* (Simpson). Hillebrandt, 1987, pl. 2, figs. 2–4.
Metaderoceras aff. *muticum* (d'Orbigny). Smith, Tipper, Taylor, and Guex, 1988, pl. 2, figs. 7–9.
Metaderoceras talkeetnaense Thomson and Smith, 1992, p. 20, pl. 6, fig. 1; pl. 7, figs. 1–5.

Description.—Evolute with a quadrate to compressed to subquadrate whorl section. The ornamentation consists of simple ribs that terminate in tubercles at the ventro-lateral shoulder. Ribbing is sharp on the innermost whorls becoming coarser with growth. Rib frequencies range from 15 ribs per half whorl up to 20 on outer whorls.



Text-figure 34.—Traces of the septal suture for species of the Eoderoceratidae at whorl heights (WH) indicated. a. *Metaderoceras evolutum* (Fucini, 1921) (GSC 98689, WH = 5.8 mm); b. *Metaderoceras*? aff. *mouterdei* Frebold, 1970 (GSC 87797, WH = 10.8 mm); c. *Metaderoceras talkeetnaense* Thomson and Smith, 1992 (GSC 98703, WH = 7.7 mm).

Type material.—Holotype: Imlay, 1981, pl. 7, figs. 12, 13. Paratypes: Imlay, 1981, pl. 7, figs. 6–10, 14, 15.

Material.—Fifty-two specimens in siltstone, mudstone and sandstone of the Ghost Creek and Fannin formations.

Discussion.—Compared with *M. talkeetnaense*, *M. mouterdei* is more evolute, has a somewhat more compressed whorl section, and stronger, less densely spaced ribs which tend to be less prorsiradiate. *M.?* aff. *mouterdei* has a much broader venter and is more coarsely and less densely ribbed throughout. *M. evolutum* is more evolute, has a more compressed whorl section, and commonly has two or three ribs merging into a tubercle whereas *M. talkeetnaense* has separate ribs which always terminate in a tubercle.

The species *Acanthopleuroceras sutherlandbrowni* was established by Frebold (1970) based on a moderately well preserved holotype from Maude Island together with some unfigured, poorly preserved external molds from elsewhere which Frebold states (1970, p. 440) did not contribute to the original description. Frebold indicated the presence of a roof-like venter bearing a blunt low keel. The outer half whorl of the holotype is non-septate and has collapsed during sediment compaction causing the venter to arch. Examination of earlier, septate whorls shows that the whorl section is compressed but the venter is nevertheless much broader than in the outer half whorl and is gently convex rather than "roof-like". A keel is not evident on any of the whorls. The assignment of Frebold's species to the genus *Acanthopleuroceras* is therefore not appropriate. It may be related to *Metaderoceras talkeetnaense* because it has similar volution and ornamentation although the whorl shape is more compressed, the expansion rate somewhat higher, and the costation sharper than is usually the case for this species. It may be a variant of *M. talkeetnaense* but more and better preserved material is needed before the issue can be resolved; should it prove to be the case, the name *sutherlandbrowni* would have priority.

Occurrence.—*M. talkeetnaense* is known from the Whiteavesi and Freboldi zones of Alaska, British Columbia, and Oregon (Imlay, 1981; Smith *et al.*, 1988; Thomson and Smith, 1992). It has also been collected from the Meridianus Zone in Argentina (Hillebrandt, 1987, 1990a).

Localities.—A11, C03, D16–18, ET1, ET2, E28, E35, E38, E40, E42, FT1, F02, GT1–3, G06–09, H10–12, I02, I07, I15.

Age.—Whiteavesi and Freboldi zones (Early Pliensbachian).

Metaderoceras sp.
Plate 17, figure 1; Text-figure 33c

Metaderoceras sp. 1, nov. Cólera, Rivas, Sequeiros, and Valenzuela, 1978, p. 311, pl. 1, fig. 1.

Description.—Large, extremely evolute, slowly expanding form. The umbilical wall is low and steep, the flanks flat and the venter broad and weakly arched producing a subquadrate whorl section. The ribs are strong, rectiradiate to gently prorsiradiate and terminate ventrally in tubercles that are weakly elongated in a spiral direction. The tubercles are situated at the angular ventro-lateral shoulder; the venter is featureless. The figured specimen is large and completely septate. Although the specimen is somewhat corroded, the septal suture is fairly simple.

Material.—Two poorly preserved specimens in coarse, calcareous sandstone occurring within the Ghost Creek Formation.

Discussion.—As far as preservation permits comparison, this form is identical to a new but unnamed species of *Metaderoceras* collected in Zaragoza Province, Spain (Cólera *et al.*, 1978). Unfortunately there is not enough well preserved material either in Spain or North America to formalize a species name. In the Queen Charlotte Islands this rare species is distinguishable from the other species of *Metaderoceras* by its extremely evolute, slowly expanding and densely ribbed shell.

Occurrence.—The Spanish material originates from the upper part of the Ibex Zone. Although not in place, both of the Queen Charlotte Island specimens were collected some distance below localities yielding acanthopleuroceratids characteristic of Ibex Zone correlatives. They were associatated with both in place and *ex situ* specimens indicating the Imlayi Zone.

Locality.—BT1.

Age.—Probably Imlayi Zone (Early Pliensbachian).

Family **DACTYLIOCERATIDAE** Hyatt, 1867

Genus **REYNESOCERAS** Spath, 1936

Aveyroniceras Pinna and Levi-Setti, 1971, p. 64.
Bettoniceras Wiedenmayer, 1977, p. 80.

Type species.—*Ammonites ragazzonii* Hauer, 1861, p. 415, pl. 1, figs. 16, 17, by original designation (Spath, 1936, p. 444).

Remarks.—The tuberculate innermost whorls are *Coeloceras*-like, whereas the outer whorls are non-tuberculate and rounded in section. Whorls may egress and ribbing become irregular in microconchs. *Aveyroniceras* is included in this genus because the type species of *Aveyroniceras* and *Reynesoceras* constitute a macroconch-microconch pair as argued by Fantini Sestini (1975), Braga (1983), and Meister (1989).

Age and distribution.—A Tethyan form ranging through beds that correlate with the Davoei and Margaritatus zones.

Reynesoceras colubriforme (Bettoni, 1900)
Plate 17, figures 4, 5; Text-figure 35b

Coeloceras colubriforme Bettoni, 1900, p. 75, pl. 7, fig. 10; Fucini, 1905, p. 294, pl. 47, figs. 13, 14; Parisch and Viale, 1906, p. 161, pl. 9, figs. 5–8.
Reynesoceras aff. *fallax* (Fucini). Du Dresnay, 1963, p. 151, pl. 2, fig. 1.
Prodactylioceras cf. *colubriforme* (Bettoni). Pinna, 1966, p. 348, pl. 10, fig. 6.
Prodactylioceras colubriforme (Bettoni). Fischer, 1971, p. 112, pl. 2, fig. 10; Cantaluppi and Montanari, 1971, p. 65, pl. 12, fig. 2.
Indunoceras (Bettoniceras) colubriforme (Bettoni). Wiedenmayer, 1977, p. 81, pl. 16, figs. 8–10.
Reynesocoeloceras (Bettoniceras) cf. *colubriforme* (Bettoni). Hillebrandt, 1981, pl. 7, fig. 9.
Aveyroniceras colubriforme (Bettoni). Smith and Tipper, 1986, fig. 2.6; Smith, Tipper, Taylor, and Guex, 1988, pl. 3, figs. 5, 6.

Description.—An evolute form that has a depressed nucleus and a broadly rounded venter to umbilical diameters of approximately 7 mm. At this point the prorsiradiate, tuberculate ribs are replaced by more densely spaced, sharper ribs that are non-tuberculate, and the whorl section becomes rounded and less depressed.

Type material.—Holotype: Bettoni, 1900, pl. 7, fig. 10. Neotype: Wiedenmayer, 1977, p. 81, pl. 16, fig. 8–10.

Material.—Twenty specimens in calcareous, fine grained sandstone of the Fannin Formation.

Measurements.—See Table 22.

Discussion.—This species differs from *R. acan-*

Table 22.—Measurements of *Reynescoceras colubriforme* (Bettoni, 1900). All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*PRHW*
GSC 87796	c50	44	23	52.3	142	32.3	13.2	30	107.1	32
	—	—	15	—	—	—	—	—	—	c29
	—	—	8	—	—	—	—	—	—	12
GSC 98595	—	25	12	48	9.5	38	7.2	28.8	131.9	23
	—	—	5.5	—	—	—	—	—	—	14

thoides (Reynès, 1868) by the narrower venter of its early whorls, its less rounded whorl sections in later whorls and its ribbing which is very regular, not quite as dense, and stronger.

Occurrence.—*Reynesoceras colubriforme* is a Tethyan species known from Italy (Wiedenmayer, 1977), Morocco (Du Dresnay, 1963), South America (Hillebrandt, 1981), and Nevada (Smith and Tipper, 1986). The species possibly arises in the Ibex Zone (Fischer, 1971) but is common in the Davoei and Margaritatus zones.

Localities.—D21, E57, I07, I14.

Age.—Freboldi and Kunae zones (Pliensbachian).

Reynesoceras aff. **colubriforme** (Bettoni, 1900)
Plate 18, figure 2

Description.—A non-septate whorl fragment from an evolute ammonite with a subrounded, depressed whorl section (WWWH=c118). Ribs are wiry, densely spaced and show asymmetry. On one side of the fragment ribs are simple; on the opposite side ribs coalesce at intervals to form radially elongate tubercles positioned near the middle of the flank.

Material.—One internal mold from the Fannin Formation.

Discussion.—This specimen differs from *R. colubriforme* only in the presence of radially elongate swellings which might be pathologic considering their asymmetry.

Locality.—E57.

Age.—Kunae Zone (Late Pliensbachian).

Reynesoceras italicum (Fucini, 1901)
Plate 18, figure 3

Coeloceras italicum Meneghini *in* Fucini, 1901a, p. 98, pl. 13, fig. 4.

Coeloceras italicum Meneghini. Fucini, 1905, p. 287, pl. 46, figs. 11–14.

Coeloceras cf. *italicum* Meneghini. Schröder, 1927, p. 98, pl. 4, fig. 10.

non *Prodactylioceras* cf. *P. italicum* (Meneghini). Imlay, 1968, p. 28, pl. 2, figs. 14–16.

Prodactylioceras italicum (Fucini). Fischer, 1971, p. 111, p. 2, fig. 12; Dommergues, Ferretti, Géczy, and Mouterde, 1983, p. 482, pl. 7, figs. 7–12.

Prodactylioceras italicum fucinii Fischer, 1971, p. 111, pl. 2, figs. 8, 11.

Aveyroniceras italicum (Meneghini). Pinna and Levi-Setti, 1971, p. 66, pl. 1, fig. 10 only.

P. (Aveyroniceras) italicum (Meneghini *in* Fucini). Géczy, 1976, p. 145, pl. 25, figs. 8, 9; pl. 26, figs. 1–4.

P. (Aveyroniceras) italicum fucinii Fischer. Géczy, 1976, p. 147, pl. 26, figs. 5, 6.

Aveyroniceras cf. *italicum* (Meneghini). Dubar and Mouterde, 1978, p. 54, pl. 3, fig. 2.

Bettoniceras italicum (Fucini). Wiedenmayer, 1980, p. 57, pl. 5, figs. 9, 10.

Prodactylioceras italicum italicum (Fucini). Imlay, 1981, p. 38, pl. 10, fig. 3.

Reynesoceras italicum (Fucini). Braga, 1983, p. 323, pl. 16, fig. 4.

Description.—An evolute, slowly expanding form with a rounded whorl section. Ribs are simple, sharp and densely spaced, reaching densities of 50 to 60 per half whorl. The small nucleus is tuberculate and densely ribbed.

Type material.—Holotype: a museum specimen labelled with its new name by Meneghini but not published until the work of Fucini (1901a, pl. 13, fig. 4).

Material.—Five specimens preserved in dark shale, siltstone and fine sandstone of the Rennell Junction Member and upper Fannin Formation sandstones.

Occurrence.—A species that is widespread in the circum-Mediterranean area where it is found in beds that correlate with the Davoei and Margaritatus zones. In the North Pacific it is known in Alaska (Imlay, 1981); Oregon (Smith, 1981), possibly the Yukon (Frebold, 1970, pl. 4, fig. 1), and Japan (Hirano, 1971).

Localities.—A13, I05, I06.

Age.—Freboldi and Kunae zones (Pliensbachian).

Reynesoceras ragazzonii (Hauer, 1861)
Plate 18, figures 6, 7; Text-figure 35d

Ammonites Ragazzonii Hauer, 1861, p. 145, pl. 1, figs. 16, 17.

Coeloceras Ragazzonii Hauer. Fucini, 1901a, p. 92, pl. 13, figs. 6, 7; Bettoni, 1900, p. 73, pl. 7, figs. 4–7; pl. 8, figs. 15–17; pl. 9, fig. 11; Fucini, 1908a, p. 94, pl. 1, fig. 25; Monestier, 1934, p. 93, pl. 6, figs. 13, 15–17, 19 and 24 only; Fucini, 1935, p. 167, pl. 38, fig. 7.

Coeloceras sub-anguinum Meneghini. Del Campana, 1900, p. 629, pl. 8, fig. 43 only.

Reynesoceras cf. *ragazzonii* (Hauer). Cantaluppi, 1966, p. 155, pl. 17, fig. 7.

Reynesoceras ragazzonii (Hauer). Cantaluppi and Brambilla, 1968, p. 294, pl. 26, fig. 11; Cantaluppi and Savi, 1968, p. 229, pl. 19, figs. 7, 8; Elmi, Atrops, and Mangold, 1974, p. 28, pl. 1, fig. 7; Fantini Sestini, 1975, p. 463, pl. 52, figs. 1–4, 6, 8; Wiedenmayer,

Table 23.—Measurements of *Reynesoceras ragazzonii* (Hauer, 1861). All measurements are in mm.

specimen no.	*DMAX*	*DPHRAG*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*PRHW*
GSC 98714	c24.7	—	c24.7	c12.3	49.8	c9.8	39.7	c7	28.3	140	22
	—	—	c18.5	c8	43.23	c10.6	57.3	c5.6	30.3	189	21
GSC 87800	27	c22	27	14	51.9	10	37	7.1	26.3	141	18
	—	—	22	9.8	44.5	10.7	48.6	6.7	30.5	160	19
	—	—	—	7	—	10.2	—	5	—	204	19

1977, p. 82, pl. 16, figs. 13, 14; Wiedenmayer, 1980, p. 61, pl. 6, figs. 1–6; Braga, 1983, p. 328, pl. 16, figs. 10–14; Meister, 1989, p. 35, pl. 5, figs. 2, 6, 7.

Reynesoceras cf. *ragazzonii* (Hauer). Imlay, 1968, p. C28, pl. 1, figs. 22–28 only.

Reynesoceras cf. *aegrum* (Fucini). Imlay, 1968, p. C28, pl. 1, figs. 20–21.

Description.—A midvolute form that egresses at umbilical diameters of 8–10 mm at which point the whorl shape becomes rounded and less depressed. Sutures are unclear but specimen GSC 87800 appears to have an incomplete body chamber approaching one whorl in length. Ribs are simple, densely spaced, and prorsiradiate on the flank. Ribbing becomes less dense or is interrupted by constrictions on the outer whorl. On the inner whorls there are small tubercles at the ventrolateral shoulder.

Type material.—Lectotype: Hauer, 1861, pl. 1, figs. 16–17 designated by Wiedenmayer (1977, p. 82).

Material.—Four specimens preserved in sandstone of the Fannin Formation.

Measurements.—See Table 23.

Discussion.—This is a microconchiate form that has been paired with the species *Aveyroniceras acanthoides* (Braga, 1983; Meister, 1989), a species not yet recognized in the Queen Charlotte Islands.

Occurrence.—This is a Tethyan species characteristic of the circum-Mediterranean countries where it is found in the Algovianum Zone of Spain and Margaritatus Zone correlatives elsewhere.

Localities.—DT1, I06.

Age.—Kunae Zone (Late Pliensbachian).

Reynesoceras sp.
Plate 18, figure 5

Description.—Evolute with a subrounded, depressed whorl section (WWWH=c110). The inner whorls on the figured specimen are only moderately well preserved but appear to be coronate. The outermost whorl fragment is non-septate. Ribs are simple, strong and prorsiradiate.

Material.—Two fragments of internal molds from the upper Fannin Formation.

Discussion.—These specimens are characterized by the coarseness of their ribbing and a relatively narrow whorl section, a combination not normally seen in the more coarsely ribbed species of *Reynesoceras* such as *R. indunense*. They could either represent a new species or be coarsely ribbed variants of *R. colubriforme* which also occurs at locality E57.

Locality.—E57, FT2.

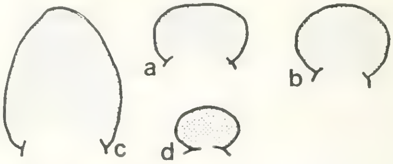
Age.—Kunae Zone (Late Pliensbachian).

Reynesoceras? sp.
Plate 18, figure 4

Description.—An evolute, slowly expanding specimen with gently rounded flanks. The ribs, which have densities of approximately 15 per half whorl, are wiry and prorsiradiate. Just beneath the umbilical seam several of the ribs bifurcate. The venter is not visible.

Material.—One slightly distorted internal mold preserved in dark siltstone interlaminated with green sandstone of the upper Fannin Formation.

Discussion.—This specimen was not in place but was associated with other ammonites and is in rock lithologically similar to the Kunae Zone outcrop adjacent to where it was found. The presence of bifurcating ribs sets it apart from all other dactylioceratids found at this level. Bifurcating ribs are normally associated with *Dactylioceras* of the Toarcian. Wiedenmayer (1980, *Aveyroniceras striatum*), Imlay (1968, *Dactylioceras* cf. *kanense, Reynesoceras* cf. *ragazzonii*), and Hirano (1973, *Dactylioceras helianthoides*) report Pliensbachian dactylioceratids with this feature but the Queen Charlotte Islands specimen appears to be most similar to two specimens of *Dactylioceras?* sp. reported by Braga (1983) from the Algovianum Zone (equivalent to



Text-figure 35.—Whorl shape cross-sections for species of the Dactylioceratidae. Figures are natural size. a,c. *Reynescoeloceras mortilleti* (Meneghini, 1875) (a. GSC 98673, c. GSC 98675); b. *Reynesoceras colubriforme* (Bettoni, 1900) (GSC 87796); d. *Reynesoceras ragazzonii* (Hauer, 1861) (GSC 87800).

the upper Margaritatus to lower Spinatum Zone) of southern Spain. The Spanish material appears to have flatter flanks and finer ornamentation, however.

Locality.—ET4.

Age.—Kunae Zone (Late Pliensbachian).

Genus **REYNESOCOELOCERAS** Géczy, 1976

Indunoceras Wiedenmayer, 1977, p. 75.
Cetonoceras Wiedenmayer, 1977, p. 79.

Type species.—*Ammonites (Stephanoceras) crassus* Young and Bird var. *indunensis* Meneghini (Meneghini, 1881, p. 72, pl. 16, fig. 4), by original designation (Géczy, 1976, p. 123).

Remarks.—Internal whorls are cadiconic and tuberculate with tri- or bifurcating ribs and this stage persists to large shell diameters compared with *Reynesoceras.* The outer whorls are serpenticonic with simple, non-tuberculate ribs. A full discussion of this genus is given by Géczy (1976, p. 123) and Wiedenmayer (1977, p. 75).

Age and distribution.—Restricted to the Tethyan Realm and ranging from the Jamesoni to the Margaritatus Zone, with most occurrences in the Davoei Zone. Reports of Sinemurian occurrences (Fischer, 1971; Wiedenmayer, 1977) were based on a misinterpretation of the biostratigraphy at Monte Cetona in Italy (Wiedenmayer, written commun., 1982).

Reynesocoeloceras cf. **incertum** (Fucini, 1905)
Plate 12, figure 1

cf. *Coeloceras incertum* Fucini, 1905, p. 312, pl. 51, figs. 4–7.
cf. *Coeloceras (Coeloceras) incertum incertum* Fucini. Fischer, 1971, p. 110, fig. 5j.
cf. *Coeloceras (Reynesocoeloceras) incertum* Fucini. Géczy, 1976, p. 131, pl. 23, figs. 4, 5.
cf. *Crucilobiceras dolosum* Wiedenmayer, 1977, p. 60, pl. 13, figs. 4, 5.
cf. *Reynesocoeloceras* sp. gr. *incertum* (Fucini). Dommergues, Ferretti, Géczy, and Mouterde, 1983, p. 475, pl. 1, figs. 23–26.
Reynesocoeloceras cf. *incertum* (Fucini). Thomson and Smith, 1992, p. 30, pl. 12, fig. 6.

Description.—An evolute, slowly expanding form with a depressed whorl section and an arched venter. Densely spaced, prorsiradiate primary ribs terminate at the ventro-lateral shoulder in sharp tubercles from which two strong secondary ribs arise. A fragment of the last part of the outermost whorl (Pl. 12, fig. 1b) shows that the ribs have become stronger and simple, and the whorl section more rounded.

Type material.—Fucini, 1905, pl. 51, figs. 4–7, Text-figure 131.

Material.—One specimen preserved in fine grained sandstone of the Rennell Junction Member.

Occurrence.—*R. incertum* is a circum-Mediterranean form found in Hungary (Géczy, 1976), Italy (Fucini, 1905), and France (Dommergues *et al.*, 1983), where it characterizes the Davoei Zone. In North America it has been reported from the Freboldi Zone of north-central British Columbia (Thomson and Smith, 1992).

Locality.—E51.

Age.—Basal Kunae Zone (Late Pliensbachian).

Reynesocoeloceras grahami, new species
Plate 12, figures 2, 5, 6

Description.—A slowly expanding, evolute form whose coronate inner whorls bear stout, prorsiradiate ribs terminating ventrally in robust tubercles. Intermediate whorls are more rounded in cross-section, display a significant increase in rib frequency and the ribs become simple. On the outermost third of a whorl of the holotype (Pl. 12, fig. 2) and one of the paratypes (Pl. 12, fig. 6) small sharp tubercles appear at the ventro-lateral shoulder and the venter flattens. The paratype figured on Plate 12, figure 5 is interpreted as a coarse-ribbed variant that never completely loses its tubercles although they do become less pronounced. On its outer one-eighth whorl, ornamentation coarsens, tubercles sharpen and become more prominent, and the last rib flares and thickens.

Type material.—Holotype: GSC 98671 (Pl. 12, fig. 2). Paratypes: GSC 98651 (Pl. 12, fig. 5), GSC 87809 (Pl. 12, fig. 6).

Material.—One external mold in fine-grained sandstone and approximately 10 specimens in a silty limestone from the Rennell Junction Member.

Measurements.—See Table 24.

Derivation of name.—This species is named after Graham Island, the large northern island of the Queen Charlotte Islands archipelago.

Discussion.—*Reynesocoeloceras grahami* is a large species, reaching diameters up to 65 mm. It differs from all other species of *Reynesocoeloceras* by the robustness of its ribbing in its early whorls which persists to umbilical diameters in excess of 15 mm.

Localities.—FT1, F02, GT3.

Age.—Freboldi Zone (Early Pliensbachian).

Reynesocoeloceras mortilleti
(Meneghini, 1875)
Plate 12, figures 3, 4, 7, 8;
Text-figures 26f, 35a,c

Ammonites (Stephanoceras) mortilleti Meneghini, 1875, appendix, pl. 4, fig. 7; 1876, appendix, p. 21, pl. 6, figs. 1, 2.
Coeloceras mortilleti Meneghini. Fucini, 1901a, p. 97, pl. 13, fig. 11; 1905, p. 288, pl. 46, fig. 10; 1908b, p. 93, pl. 3, figs. 30, 31.
Prodactylioceras cf. *P. mortilleti* (Meneghini). Imlay, 1968, p. C29, pl. 2, figs. 11–13, 19, 20.

Table 24.—Measurements of *Reynesocoeloceras grahami,* new species. All measurements are in mm.

specimen no.	DMAX	D	UD	U	WW	WWD	WH	WHD	WWWH	PRHW
GSC 99047	c49	c49	29	59.2	—	—	10	20.4	—	42
		—	19	—	—	—	—	—	—	22
GSC 98671	50	50	30	60	15.9	31.8	10.5	21.0	151.4	38
(holotype)		—	27	60	c12.5	27.8	10	22.2	125	40
		45	16	—	—	—	—	—	—	15
		—	4.5	—	—	—	—	—	—	9
GSC 87809	c46	c46	29	63	13.5	29.3	9.2	20.0	146.7	37
(paratype)		—	25	—	—	—	—	—	—	35
		—	17	—	—	—	—	—	—	16
		—	10	—	—	—	—	—	—	14
		—	6	—	—	—	—	—	—	11
GSC 98651	55	55	32	58.2	15.7	28.5	13	23.6	120.8	32
(paratype)		47	28	59.6	14	29.8	10	21.3	140	31
		—	18	—	—	—	—	—	—	12
		—	10	—	—	—	—	—	—	10

Aveyroniceras italicum (Meneghini). Pinna and Levi Setti, 1971, p. 66, pl. 1, fig. 11 only.

Indunoceras (Bettoniceras) mortilleti (Meneghini). Wiedenmayer, 1977, p. 80, pl. 16, fig. 7.

Reynesocoeloceras (Bettoniceras) cf. *mortilleti* (Meneghini). Hillebrandt, 1981, p. 512, pl. 7, figs. 10, 11.

Reynesoceras mortilleti (Meneghini). Braga, 1983, p. 330, pl. 16, fig. 15.

Description.—An evolute form that has a coronate whorl section until umbilical diameters of approximately 15 to 20 mm. Regularly spaced tubercles occur at the angular ventro-lateral shoulder where some primary ribs loop together; two or, more commonly, three secondary ribs arch gently forward from the tubercles across the venter. Between the tubercles ribs are simple.

As growth proceeds, the whorl shape gradually becomes less depressed and more rounded with the tubercles becoming irregularly spaced and radially elongate. Outer whorls are simply and densely ribbed; tubercles are rare.

Type material.—Lectotype: Meneghini, 1876 (appendix), pl. 6, fig. 2 refigured by Fucini, 1908b, pl. 3, fig. 30. Paralectotypes: Meneghini, 1875 (appendix), pl. 4, fig. 7; 1876 (appendix), pl. 6, fig. 1.

Material.—Fifty-eight specimens, mostly fragments, preserved in fine grained calcareous sandstone and siltstone of the Fannin Formation.

Measurements.—See Table 25.

Occurrence.—*Reynesocoeloceras mortilleti* is a Tethyan species ranging from the Jamesoni Zone to the Margaritatus Zone (Wiedenmayer, 1977) in the circum-Mediterranean area. In South America it occurs in beds equivalent to the Margaritatus zone (Hillebrandt, 1981, 1987).

Localities.—B5, DT1, D22, E52, FT2, GT3, I06, I15.

Age.—Kunae and, rarely, the Freboldi Zone (Pliensbachian).

Reynesocoeloceras spp.

Plate 11, figures 7, 8

Description.—Specimen GSC 98668 (Pl. 11, fig. 7) is a distorted external mold of an evolute form that had a depressed *Coeloceras*-like whorl section. Strong primary ribs terminate at the ventro-lateral shoulder in tubercles from which two or three weaker secondary ribs develop; intercalated secondary ribs also appear to be present.

Specimen GSC 98869 (Pl. 11, fig. 8) also has a depressed, *Coeloceras*-like whorl section but the ventrolateral shoulders are less sharp. Ribbing is very strong and the tubercles at the ventro-lateral shoulder are blunt and slightly radially elongate. Some ribs remain

Table 25.—Measurements of *Reynesocoeloceras mortilleti* (Meneghini, 1875). All measurements are in mm.

specimen no.	DMAX	D	UD	U	WW	WWD	WH	WHD	WWWH	PRHW	SRHW	THW
GSC 98673	34	31	15	48.4	16.4	52.9	9.2	29.7	178.3	26	37	c8
GSC 98674	27	24.5	12	50	—	—	7	—	—	23	32	6
	—	—	9	—	13.5	—	5.5	—	245.5	—	—	—
GSC 98675	—	—	c29	—	c20.6	—	c14.9	—	138.3	—	—	—
GSC 99019	—	—	c20	—	c18.1	—	c12.4	—	146	25	41	c12

Table 26.—Measurements of *Amaltheus stokesi* (Sowerby, 1818). All measurements are in mm.

specimen no.	*WW*	*WH*	*WWWH*
GSC 98717	c5.5	c9.5	c57.9

simple while others give rise to two secondary ribs. The primary and secondary ribs are equally strong.

Material.—Three external molds preserved in calcareous sandstone.

Discussion.—These specimens are placed in *Reynesocoeloceras* because they are moderately large and yet still retain their *Coeloceras*-like whorl shape and coarse ribbing. The state of preservation does not permit a confident species assignment.

Occurrence.—Specimen GSC 98668 was not found in place but was associated with a Whiteavesi Zone fauna thought to originate from the Rennell Junction Member of the Fannin Formation (loc. GT1). This form may also be present at locality I02. Specimen GSC 98669 was found at locality E40 from the Whiteavesi Zone of the Rennell Junction beds.

Family **AMALTHEIDAE** Hyatt, 1867

Genus **AMALTHEUS** de Montfort, 1808

Proamaltheus Lange, 1932, p. 238.
Nordamaltheus Repin, 1968, p. 111.

Type species.—*Amaltheus margaritatus* de Montfort, 1808, p. 91, by monotypy.

Age and distribution.—A Boreal genus characteristic of the Margaritatus and Spinatum zones. Only five specimens (including the material described below) have been recorded from the allochthonous terrane Wrangellia (Imlay, 1981).

Amaltheus stokesi (J. Sowerby, 1818)
Plate 19, figure 1; Plate 20, figure 3
Text-figure 36a-b

Ammonites stokesi Sowerby, 1818, p. 205, pl. 191.
Amaltheus cf. *A. nudus* (Quenstedt). Imlay, 1955, p. 87, pl. 10, fig. 5.
Amaltheus stokesi (J. Sowerby). Howarth, 1958, p. 3, pl. 1, figs. 5, 7, 12–14; pl. 2, figs. 1, 3, 10; Dean, Donovan and Howarth, 1961, pl. 70, fig. 2; Frebold, 1964a, p. 9, pl. 2, figs. 2–6; Frebold, Mountjoy and Tempelman-Kluit, 1967, p. 14, pl. 1, figs. 1–3, 5, 7; Géczy, 1967, p. 93, pl. 25, fig. 1; Frebold, 1970, p. 3, fig. 1; Repin, 1974, p. 55, pl. 1, figs. 4–9; Frebold, 1975, p. 10, pl. 4, figs. 3, 4; Wiedenmayer, 1980, p. 51, pl. 2, fig. 11; Sey and Kalacheva, 1980, p. 71, pl. 1, figs. 4, 6–8, 11, 13; Imlay, 1981, p. 37, pl. 10, figs. 23, 24, 27, 28; Braga, Comas-Rengifo, Goy, and Rivas, 1985, pl. 1, figs. 6–7; Poulton, 1991, p. 18, pl. 8, figs. 1–8.
Amaltheus cf. *A. stokesi* (Sowerby). Frebold, 1966, p. 2, pl. 1, figs. 1–4.
Amaltheus cf. *margaritatus* de Montfort. Repin, 1968, p. 108, pl. 35.
Amaltheus cf. *A. stokesi* (Sowerby). Hirano, 1971, p. 101, pl. 17, figs. 11a,b.
Amaltheus (Amaltheus) stokesi (Sowerby). Schlegelmilch, 1976, p. 70, pl. 34, fig. 7.
Amaltheus (Proamaltheus) stokesi (Sowerby). Dagis, 1976, p. 21, pl. 10, figs. 5–7.

Description.—Involute form with an ellipsoidal whorl section. The low umbilical wall rounds rapidly into the gently convex flanks. The venter bears a low crenulate keel consisting of forwardly directed chevrons. The prorsiradiate primary ribs curve gently backwards across the flanks then fade somewhat as they project towards the venter; a few primaries bifurcate. Neither the aperture nor the septal suture is visible.

Type material.—Holotype: J. Sowerby, 1818, pl. 191 refigured by Howarth, 1958, pl. 1, fig. 7.

Material.—Two specimens in limestone and calcareous sandstone of the upper Fannin Formation.

Measurements.—See Table 26.

Because of the poor preservation, exact rib counts cannot be made but the density appears to fall within the ribbing density envelope for *A. stokesi* as illustrated by Howarth (1958, fig. 4).

Discussion.—*Amaltheus stokesi* has been treated in detail by Howarth (1958).

Occurrence.—*Amaltheus stokesi* is a species distributed widely throughout the Boreal Realm (Canada, the former Soviet Union, northwest Europe, Alaska) as well as in mixed Tethyan/Boreal faunas of Italy, Hungary, Canada, Japan, and the former Soviet Union. It is characteristic of the lowest subzone (the Stokesi subzone) of the Margaritatus Zone in northwest Europe and it appears to be consistently low in the Upper Pliensbachian in other parts of the world.

Localities.—FT2, GT4.

Age.—Kunae Zone (Late Pliensbachian).

Table 27.—Measurements of *Amaltheus viligaensis* (Tuchkov, 1954). All measurements are in mm.

specimen no.	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WW-WH*	*PR-HW*
GSC 87805	24.9	6.9	27.7	6.9	27.7	10.3	41.4	67	13

Amaltheus viligaensis (Tuchkov, 1954)
Plate 20, figure 2; Text-figure 36c

Acanthopleuroceras viligaensis Tuchkov, 1954, p. 109, pl. 2, fig. 4.
Amaltheus (Nordamaltheus) viligaensis (Tuchkov). Repin 1968, p. 111, pl. 33, figs. 1–5; pl. 37, fig. 3; 1974, p. 62, pl. 5, figs. 6, 8, 10; pl. 7, figs. 2–5.
Amaltheus (Nordamaltheus?) bulunensis Repin, 1968, p. 111, pl. 35, fig. 2.
Amaltheus (Nordamaltheus) aff. *bulunensis* Repin, 1968, p. 112, pl. 36, fig. 1.
Amaltheus (Nordamaltheus) bulunensis Repin, 1974, p. 63, pl. 5, figs. 1–2.

Amaltheus (Nordamaltheus) brodnensis Repin, 1974, in part, p. 64, pl. 5, fig. 4; pl. 66, figs. 1–5.
Amaltheus (Nordamaltheus) brodnensis ventrocalvus Repin, 1974, p. 65, pl. 5, figs. 3, 5, 7, 9.
Amaltheus (Proamaltheus) viligaensis (Tuchkov). Dagis, 1976, p. 27, pl. 16, figs. 1–8; pl. 17, figs. 1, 2.
Amaltheus ex gr. *viligaensis* (Tuchkov). Sey and Kalacheva, 1980, p. 73, pl. 2, figs. 2, 3.
Amaltheus viligaensis (Tuchkov). Smith, Tipper, Taylor, and Guex, 1988, pl. 5, figs. 5, 6.

Description.—Involute, ellipsoidal whorl section; umbilical wall very low passing into convex flanks; venter rounded. A broad, low crenulate keel formed by forwardly inclined chevrons begins to develop on the outer quarter whorl. In earlier whorls the venter is rounded and featureless. Primary ribs are prorsiradiate, arching gently backwards to become rectiradiate near the middle of the flank. Ribs become obsolete on the upper flank except on the outer quarter where the ribs fade but can be seen projecting strongly onto the venter to form chevrons; some chevrons form by intercalation. Weak striations parallel to the primary ribs are evident on the lower half of the flank on the outer quarter whorl.

No sutures are visible but at least the outer half whorl probably represents the body chamber.

Type material.—Holotype: Tuchkov, 1954, pl. 2, fig. 4. Neotype: Repin, 1974, pl. 7, fig. 2.

Material.—One internal mold preserved in calcareous sandstone of the upper Fannin Formation.

Measurements.—See Table 27.

Discussion.—If the development of a keel is a function of maturity in *A. viligaensis,* as suggested by Repin (1974), then the Queen Charlotte Island specimen is a microconch because it is only a third of the diameter of some of the Russian specimens. *A. viligaensis* differs from *A. stokesi* by its wider whorl section and weak to absent keel.

Occurrence.—*A. viligaensis* is a Boreal species restricted to the northern Pacific. In Russia it is characteristic of assemblages correlated broadly with the Spinatum Zone of northwest Europe (Repin, 1974; Dagis, 1976; Sey and Kalacheva, 1980). In outcrops to the north of Vladivostok, the species is associated with *Paltarpites* (=*Protogrammoceras (P.) skidegatense* n. sp.) and *Lioceratoides serotinum* (Bettoni, 1900).

Locality.—E62.

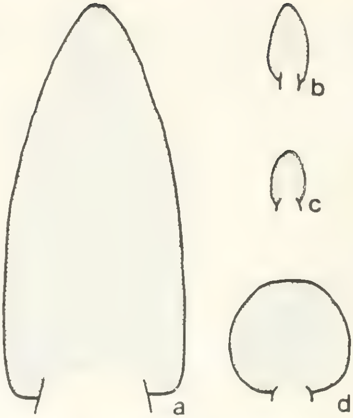
Age.—Carlottense Zone (Late Pliensbachian).

Family **LIPAROCERATIDAE** Hyatt, 1867

Genus **LIPAROCERAS** Hyatt, 1867

Subgenus **BECHEICERAS** Trueman, 1918

Anisoloboceras Trueman, 1918, p. 263.
Becheoceras Dacqué, 1934, p. 292.



Text-figure 36.—Whorl shape cross-sections for species of the Amaltheidae and Liparoceratidae. Figures are natural size. a,b. *Amaltheus stokesi* (J. Sowerby, 1818) (a. GSC 98711, b. GSC 98717); c. *Amaltheus viligaensis* (Tuchkov, 1954) (GSC 87805); d. *Liparoceras (Beicheiceras) bechei* (J. Sowerby, 1821) (GSC 78715).

Type species.—*Ammonites Bechei* J. Sowerby, 1821, p. 143, pl. 280 by original designation (Trueman, 1918, p. 261). A neotype was designated by Donovan and Forsey (1973, p. 13, pl. 2, fig. 4) and refigured by Schlegelmilch (1976, pl. 31, fig. 5).

Remarks.—The shell is inflated and involute with two rows of tubercles and subdued costation. A discussion of the subgenus is given by Spath (1938).

Age and distribution.—The subgenus ranges through the Davoei and Margaritatus zones in northwest Europe, where it was first described. Although rarely abundant, the subgenus is also widespread throughout the Mediterranean region, southern Europe, Indonesia, and the Americas where it may range stratigraphically lower, perhaps as low as the Jamesoni Zone (Géczy, 1976).

Liparoceras (Becheiceras) bechei
(J. Sowerby, 1821)
Plate 19, figure 2; Plate 20, figure 1;
Text-figure 36d

Ammonites Bechei J. Sowerby, 1821, p. 143, pl. 280.
Liparoceras rotticum Krumbeck, 1922, p. 198, pl. 18, figs. 1, 2.
Liparoceras Bechei (Sowerby). Schröder, 1927, p. 225, pl. 12, figs. 6, 7.
Liparoceras (Becheiceras) bechei (J. Sowerby). Spath, 1938, p. 74, pl. 8, fig. 2; pl. 11, figs. 1, 2, pl. 24, fig. 1; Donovan and Forsey, 1973, p. 13, pl. 2, fig. 4; Géczy, 1976, p. 100, pl. 19, figs. 2, 3; Wiedenmayer, 1977, p. 70, pl. 155, figs. 5, 6; Pérez, 1982, pl. 20, fig. 11; Meister, 1986, p. 63, pl. 13, fig. 4.

Table 28.—Measurements of *Liparoceras* (*Becheiceras*) *bechei* (J. Sowerby, 1821). All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*THW*
GSC 98715	38	38	4	10.5	c20.5	53.9	23.5	61.8	87.2	18
GSC 98684	16	16	2	12.5	9.5	59.4	8.7	54.4	109.2	—

Becheiceras cf. *B. bechei* (Sowerby). Frebold, 1964a, p. 8, pl. 3, fig. 1; pl. 4, fig. 1; pl. 5, fig. 1.

Liparoceras (Becheiceras) cf. *L. (B.) bechei* (Sowerby). Imlay, 1968, p. C27, pl. 1, figs. 18, 19.

Becheiceras gr. *bechei* (Sowerby). Blau and Meister, 1991, p. 179, pl. 4, fig. 5.

Description.—Involute form with rounded umbilical wall, flanks and venter. Ornamentation, which is very weak, consists of spiral striations to shell diameters of at least 15 mm, dense ribs and two rows of weak tubercles.

Type material.—Holotype: J. Sowerby, 1821, pl. 280. Neotype: Donovan and Forsey, 1973, p. 13, pl. 2, fig. 4.

Material.—Seven specimens preserved in limestone and calcareous sandstone of the Fannin Formation.

Measurements.—See Table 28.

Occurrence.—A cosmopolitan species, perhaps more abundant in northwest Europe, that Spath (1938) states is characteristic of the upper part of the Davoei Zone. Wiedenmayer (1977), however, has recognized the species from the Margaritatus Zone while Géczy (1976) has questionable occurrences in the Ibex and Jamesoni zones. Pérez (1982) has collected the species from the Upper Pliensbachian of Chile.

Localities.—ET1, ET4, E32, FT2, GT4.

Age.—Whiteavesi to Kunae zones (Pliensbachian).

Genus **OISTOCERAS** Buckman, 1911

Type species.—*Ammonites figulinus* Simpson, 1855, p. 47, by original designation (Buckman, 1911, p. 4, pl. 26A).

Remarks.—Species of *Oistoceras* are evolute and bear simple ribs that show a pronounced forward flexure on the tabulate venter. Most species become bituberculate and less densely ribbed at large shell diameters.

Age and distribution.—This genus (through *O. figulinum*) is thought to be the root-stock of the amaltheid radiation (Howarth, 1958). The genus is known throughout northern Europe (Spath, 1938; Hoffmann, 1982) with occurrences also in Portugal (Mouterde *et al.*, 1983), southern France (Meister, 1986), Spain (Braga *et al.*, 1985), and Hungary (Géczy, 1976). It is characteristic of the Davoei and Margaritatus zones.

Oistoceras compressum, new species
Plate 5, figures 3–12

Uptonia? sp. B. Imlay, 1981, p. 37, pl. 9, figs. 5–7.

(?) Oistoceras sp. Braga, Comas-Rengifo, Goy, and Rivas, 1985, pl. 1, fig. 5.

Uptonia? sp. Thomson and Smith, 1992, p. 15, pl. 4, figs. 1, 2.

Description.—Evolute, slowly expanding form with a compressed whorl section. The ribs are simple, sharp, densely spaced, and non-tuberculate. The ribs are subrectiradiate to prorsiradiate across the flanks but swing strongly forward onto the venter where they form chevrons. The ventral ribbing varies from fairly weak in some cases (Pl. 5, figs. 7 and 12) to very strong in most cases. In some specimens evidence of whorl egression, a strengthening of the ventral ornamentation and a slight change in whorl shape to less compressed (*e.g.*, Pl. 5, figs. 5 and 10) suggest that maturity is reached at a small shell diameter.

Type material.—Holotype: GSC 99039 (Pl. 5, fig. 5). Paratypes: GSC 98625 (Pl. 5, fig. 3), GSC 98696 (Pl. 5, fig. 4), GSC 98710 (Pl. 5, fig. 6), GSC 98738 (Pl. 5, fig. 7), GSC 99027 (Pl. 5, fig. 8), GSC 99038 (Pl. 5, fig. 9), GSC 99041 (Pl. 5, fig. 10), GSC 99042 (Pl. 5, fig. 11), GSC 99043 (Pl. 5, fig. 12).

Material.—Approximately 75 internal molds in calcareous sandstone and siltstone of the Rennell Junction Member.

Measurements.—See Table 29.

Derivation of name.—In reference to the characteristically compressed whorls.

Discussion.—This has been a difficult form to place taxonomically since, although it bears a resemblance to some species of the genus *Uptonia* to which it has been questionably referred in the past (Imlay, 1981; Thomson and Smith, 1992; Smith *et al.*, 1988), it is now quite clear that it occurs much later than *Uptonia* as presently understood. *Uptonia* is characteristic of the Jamesoni Zone whereas *O. compressum* occurs in beds correlative with the Davoei Zone.

This species is placed in *Oistoceras* rather than *Uptonia* because of: (1) its resemblance to densely ribbed species of *Oistoceras* such as *O. angulatum* (Quenstedt) (Mouterde *et al.*, 1983, p. 208, pl. 12, figs. 17, 18; pl. 13, fig. 3); (2) the marked forward inflection of the ribs onto the venter, much more strongly than is seen in *Uptonia*; (3) its high stratigraphic position, consistently above the acanthopleuroceratids and with *Dubariceras freboldi* and other elements of the Freboldi Zone.

The species differs from all other species of *Oisto-*

Table 29.—Measurements of *Oistoceras compressum*, new species. All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*PRHW*
GSC 98696	31	29.0	11.7	40.3	6.3	21.7	9.5	32.8	66.3	22
GSC 99039	24.4	24.4	10.3	42.2	5.5	22.5	6.4	26.2	85.9	25
	—	20.0	7.4	37.0	4.5	22.5	6.2	31.0	72.6	20
GSC 98738	24.1	24.1	8.4	34.9	5.9	24.5	8.1	33.6	72.8	21
	—	—	6.0	—	3.9	—	5.0	—	78.0	17
GSC 99038	16.2	16.2	c6.5	40.1	—	—	—	—	—	24
	—	—	3.9	—	3.6	—	3.8	—	94.7	21
GSC 99041	—	24.6	10.0	40.7	5.5	22.4	7.3	29.7	75.3	19
GSC 99042	—	20.0	8.1	40.5	4.3	21.5	6.2	31.0	69.4	27
GSC 99043	14.4	14.4	5.2	36.1	3.5	24.3	4.4	30.6	79.5	19
MEAN				39.0		22.8		30.7	77.2	
ST. DEV.				2.6		1.2		2.4	8.7	

ceras by its combination of dense, fine ribbing and compressed whorl section.

Localities.—ET3, FT1, F02.

Age.—Freboldi Zone (Early Pliensbachian).

Superfamily **HILDOCERATACEAE** Hyatt, 1867

Family **HILDOCERATIDAE** Hyatt, 1867

Subfamily **ARIETICERATINAE** Howarth, 1955

Genus **ARIETICERAS** Seguenza, 1885

Seguenziceras Levi, 1896, p. 272.
Meneghinia Fucini, 1931, p. 118.
Protoarieticeras, Cantaluppi, 1970, p. 40.
Pseudoarieticeras Cantaluppi, 1970, p. 40.
Géczya Fantini Sestini, 1977, p. 710.

Type species.—*Ammonites algovianus* Oppel, 1862, p. 137 (Seguenza, 1885, p. 67). Lectotype and paralectotype (the latter refigured from Schröder, 1927) designated and figured by Wiedenmayer (1977).

Remarks.—Fairly evolute forms with a quadrate to elliptical whorl section, unicarinate venter and simple, straight to gently sinuous ribs.

Age and distribution.—A widespread genus most characteristic of the Tethyan Realm where it is restricted to the Margaritatus and Spinatum zones. Also known from the Americas (Hillebrandt, 1973, 1981; Imlay, 1968, 1981; Frebold, 1964a), Japan (Hirano, 1973), and Russia (Sey and Kalacheva, 1980).

Arieticeras aff. **algovianum** (Oppel, 1862)

Plate 20, figures 11, 12

aff. *Ammonites algovianus* Oppel, 1862, p. 137.
aff. *Arieticeras algovianum* (Oppel). Wiedenmayer, 1977, pl. 16, figs. 15, 16; Frebold, 1964a, p. 13, pl. 3, figs. 4, 5, pl. 4, fig. 2; 1970, p. 443, pl. 2, fig. 1.
Arieticeras cf. *algovianum* (Oppel). Frebold, 1964a, p. 13, pl. 3, fig. 3, pl. 5, fig. 3; Imlay, 1968, p. 34, pl. 4, figs. 1–8; 1981, p. 40, pl. 10, figs. 16–20.
Arieticeras cf. *domarense* (Oppel). Imlay, 1981, p. 39, pl. 10, figs. 1, 2, 9, 10.
Arieticeras aff. *algovianum* (Oppel). Thomson and Smith, 1992, p. 36, pl. 14, figs. 1–7.

Description.—Evolute with a compressed whorl section bearing a high keel bordered by shallow sulci. Ribs are strong, slightly sinuous and gently rursiradiate in trend.

Type material.—Lectotypes for *Arieticeras algovianum* were designated by Wiedenmayer, 1977, p. 86, pl. 16, fig. 15 (paralectotype) and 16 (lectotype).

Material.—Thirteen internal molds, mostly fragments, preserved in calcareous sandstone of the upper Fannin Formation.

Discussion.—This species is related to *A. algovianum* from which it differs by its slightly greater expansion rate. The species differs from *A.* aff. *domarense* in its higher expansion rate and coarser, more sinuous ribbing; from *A.* cf. *ruthenense* by its less dense, coarser, more sinuous ribbing; from *A. disputabile* by its greater expansion rate end ribbing density; from *A.* cf. *micrasterias* by its less coarse ribbing and more compressed whorl shape; and from *A. lupheri* which has denser ribbing that is strongest on the upper part of the flank.

Occurrence.—This material is conspecific with specimens of *Arieticeras* cf. and aff. *algovianum* from northern British Columbia as figured by Frebold (1964a, 1970) and Thomson and Smith (1992). In Europe, *A. algovianum* is common in the Upper Pliensbachian of the circum-Mediterranean area.

Locality.—I14, I17.

Age.—Kunae Zone (Late Pliensbachian).

Arieticeras disputabile (Fucini, 1908)

Plate 20, figure 5; Plate 21, figure 2
Text-figures 37b, 38o

Hildoceras disputabile Fucini, 1908b, p. 66, pl. 2, figs. 34–36.
Arieticeras gerardi Monestier, 1934, p. 77, pl. 8, figs. 35–37.
Arieticeras apertum Monestier, 1934, p. 50, pl. 10, figs. 21, 23, 37 and 47 only.

Table 30.—Measurements of *Arieticeras disputabile* (Fucini, 1908). All measurements are in mm.

specimen no.	*DM-AX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WW-WH*	*PR-HW*
GSC 98719	c20	16.8	7.2	43	4.4	26.2	5.0	29.8	88	11

non *Arieticeras disputabile* (Fucini). Monestier, 1934, p. 67, pl. 10, figs. 5, 6; pl. 11, fig. 10; Wiedenmayer, 1980, p. 112, pl. 18, figs. 25–28.

Arieticeras disputabile (Fucini). Fantini Sestini, 1977, p. 730, pl. 35, figs. 5, 7; Braga, 1983, p. 219, pl. 9, figs. 20–23; Braga, Comas-Rengifo, Goy and Rivas, 1985, pl. 2, fig. 9; Meister, 1989, p. 43, pl. 6, fig. 6.

Description.—A very evolute form with a compressed subquadrate to subelliptical whorl section. The low keel is bordered by smooth areas that become incipient sulci on the outer half whorl of the specimen figured on Plate 20, figure 5. The inner whorls are smooth with ribs beginning at an umbilical diameter of approximately 5 mm. The ribs are weakest on the lower part of the flank, stronger and rursiradiate on the rest of the flank and projected onto the venter where they quickly fade.

Type material.—Lectotype: Fucini, 1908b, pl. 2, figs. 35–36.

Material.—Two internal molds and a fragment of an internal mold preserved in calcareous sandstone of the upper Fannin Formation.

Measurements.—See Table 30.

Discussion.—The specimen figured on Plate 20, figure 5 is less compressed and more coarsely ribbed than the specimen figured on Plate 21, figure 2. It compares most favorably with *Arieticeras gerardi* Monestier considered a junior synonym of *A. disputabile.*

Occurrence.—From the Margaritatus Zone of Italy (Fucini, 1908), southern France (Meister, 1989) and Spain (Braga, 1983).

Localities.—FT2, GT4, I14.

Age.—Kunae Zone (Late Pliensbachian).

Arieticeras aff. **domarense** (Meneghini, 1867)

Plate 20, figure 4; Text-figure 37a

aff. *Ammonites (Harpoceras) domarensis* Meneghini, 1867, p. 7; 1870, pl. 1, figs. 4–6, 9.

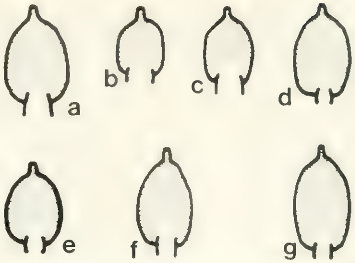
aff. *Hildoceras (Arieticeras) domarense* (Meneghini). Bettoni, 1900, p. 56, pl. 5, fig. 3.

aff. *Arieticeras domarense* (Meneghini). Monestier, 1934, p. 62, pl. 7, figs. 23, 25, 27, 29, 30; pl. 11, fig. 15; Fantini Sestini, 1962, p. 520, pl. 39, figs. 5, 6.

Arieticeras sp. Corvalan, 1962, p. 187, pl. 3, fig. 6.

Arieticeras cf. *algovianum* (Oppel). Hallam, 1965, p. 1488 (reference to Corvalan, 1962, pl. 3, fig. 6; specimen figured by Smith, Tipper, Taylor and Guex, 1988, pl. 4, figs. 10, 11).

Arieticeras cf. *domarense* (Meneghini). Imlay, 1968, p. 33, pl. 4, figs. 9–12; Imlay, 1981, p. 39, pl. 10, figs. 6–8 and 11–14 only.



Text-figure 37.—Whorl shape cross-sections for species of the Arieticeratinae. All figures are ×2. a. *Arieticeras* aff. *domarense* (Meneghini, 1867) (GSC 98718); b. *Arieticeras disputabile* (Fucini, 1908) (GSC 98719); c. *Fieldingiceras fieldingii* (Reynés, 1868) (GSC 98728); d. *Arieticeras lupheri* Imlay, 1968 (GSC 98721); e,f. *Leptaleoceras* sp. (e. GSC 98602, f. GSC 98604); g. *Fieldingiceras pseudofieldingii* (Fucini, 1904) (GSC 98587).

Description.—Very evolute and slowly expanding with a compressed, subquadrate to ovate whorl section (WWWH=c90) bearing a sharp keel bordered by weak sulci. Ribs are wiry, rectiradiate to gently rursiradiate and fairly densely spaced.

Type material.—Syntypes for *Arieticeras domarense*: Meneghini, 1870, pl. 1, figs. 4–6, 9.

Material.—Ten specimens, mostly incomplete, preserved in sandstone of the upper Fannin Formation.

Discussion.—This species appears to be conspecific with material from elsewhere in North America described as *A.* cf. *domarense* (Imlay, 1968, 1981) and it is certainly closely related to this species. The slightly squarer whorl section led Wiedenmayer (1980, p. 125) tentatively to include the form in his new genus *Oregonites,* but the sulci are too weak, the whorl section too compressed and the ribs too fine and regular.

Occurrence.—*A. domarense* is an Upper Pliensbachian, northern Mediterranean species. *A.* aff. *domarense* is known from the Kunae Zone of Alaska (Imlay, 1981), Oregon (Imlay, 1968), and Nevada (Corvalan, 1962; Smith *et al.,* 1988).

Localities.—ET5, E52, E59, I06 and I17.

Age.—Kunae and Carlottense zones (Late Pliensbachian).

Arieticeras lupheri Imlay, 1968

Plate 20, figures 6, 7; Text-figure 37d

Arieticeras lupheri Imlay, 1968, p. C34, pl. 4, figs. 13–28; Wiedenmayer, 1977, p. 84, pl. 17, fig. 2; Wiedenmayer, 1980, p. 113, pl. 19, figs. 19–22.

Description.—Evolute form with a low, weakly sulcate keel. The umbilical wall is low and steep, the flanks flat and the venter broadly rounded. The inner whorls are smooth with ribbing on the outer whorls confined

Table 31.—Measurements of *Arieticeras lupheri* Imlay, 1968. All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*PRHW*
GSC 98720	25	c19	7	36.8	5.0	26.3	6.6	34.7	75.8	c14
GSC 98721	c26	19.5	8	41.0	5.1	26.2	6.5	33.3	78.5	c16
GSC 99020	—	18.5	6.3	34.1	c4.9	26.5	6.5	35.1	75.4	13

to the upper part of the flank. Ribs are densely spaced and rectiradiate to gently rursiradiate in trend.

Type material.—Holotype: Imlay, 1968, pl. 4, figs. 24, 25, 28. Paratypes: Imlay, 1968, pl. 4, figs. 13–24, 26, 27.

Material.—Nine specimens in calcareous sandstone of the upper Fannin Formation.

Measurements.—See Table 31.

Discussion.—Because the specimens available for study are small (maximum shell diameter=c25 mm), it is difficult to make comparisons with the type material which reaches shell diameters of 60 mm or more and undergoes a modification of whorl shape and ornamentation during ontogeny. The Queen Charlotte Island material, however, does show the compressed subquadrate whorl section and ornamentation characteristic of *A. lupheri* at small diameters.

Occurrence.—*A. lupheri* has been reported from the equivalents of the Margaritatus Zone in Switzerland (Wiedenmayer, 1977, 1980) and Oregon (Imlay, 1968).

Localities.—DT1, I06.

Age.—Kunae Zone (Late Pliensbachian).

Arieticeras cf. **micrasterias** (Meneghini, 1874)

Plate 20, figure 8

cf. *Ammonites (Harpoceras) mercati* Hauer var. *micrasterias* Meneghini, 1874, appendix, pl. 2, fig. 14 only; 1875, appendix, p. 3.
cf. *Hildoceras rimotum* Fucini, 1905, p. 282, pl. 45, fig. 12; 1908b, p. 47, pl. 1, figs. 47, 48.
cf. *Hildoceras micrasterias* Meneghini. Fucini, 1908a, p. 12, pl. 2, fig. 13; 1908b, p. 48, pl. 1, figs. 49–51.
cf. *Hildoceras simplex* Fucini, 1908b, p. 45, pl. 1, fig. 39–41.
cf. *Arieticeras micrasterias* (Meneghini). Fucini, 1931, p. 113, pl. 23, fig. 9; Monestier, 1934, p. 71, pl. 7, figs. 11–13, pl. 10, figs. 7–9; Fantini Sestini, 1962, p. 525, pl. 39, fig. 12; 1977, p. 728, pl. 35, figs. 3, 6; Braga, 1983, p. 222, pl. 9, figs. 24, 25; Meister, 1989, p. 44, pl. 6, fig. 8.
cf. *Arieticeras rimotum* (Fucini). Monestier, 1934, p. 71, pl. 10, fig. 55; Ferretti, 1972, p. 109, pl. 14, fig. 2.
cf. *Arieticeras simplex* (Fucini). Wiedenmayer, 1977, p. 112, pl. 18, figs. 35–28; 1980, p. 116, pl. 21, figs. 9–12.
Arieticeras cf. *simplex* (Fucini). Hillebrandt, 1981, p. 516, pl. 8, fig. 7.
Arieticeras sp. Imlay, 1981, p. 40, pl. 10, fig. 21.

Description.—Evolute and slowly expanding. The umbilical wall is steep, the umbilical shoulder abrupt and the flanks flat. The flat venter bears a keel bordered by sulci. The nucleus is smooth to an umbilical diameter of approximately 3 mm; the rest of the whorls bear strong, simple ribs that are gently rursiradiate.

Type material.—Lectotype: Meneghini, 1874, pl. 2, fig. 14 (Braga, 1983).

Material.—Two external and one internal mold in sandstone of the upper Fannin Formation.

Occurrence.—A species characteristic of the Upper Pliensbachian of the circum-Mediterranean area (Braga, 1983; Wiedenmayer, 1980) with other possible occurrences in Alaska (Imlay, 1981) and South America (Hillebrandt, 1981) under the names listed in the above synonymy.

Localities.—D22, I17.

Age.—Kunae Zone (Late Pliensbachian).

Arieticeras cf. **ruthenense** (Reynès, 1868)

Plate 20, figures 9, 10

cf. *Ammonites ruthenense* Reynès, 1868, p. 94, pl. 2, fig. 4.
cf. *Arieticeras ruthenense* (Reynès). Monestier, 1934, p. 59, pl. 8, figs. 2, 4, 5; Wiedenmayer, 1980, p. 115, pl. 20, figs. 21–24, pl. 21, figs. 1, 2; Meister, 1989, p. 52, pl. 8, figs. 3–6, pl. 9, figs. 1–5.
non *Arieticeras* aff. *ruthenense* (Reynès). Frebold, 1964a, p. 14, pl. 4, figs. 3, 4 (=*Leptaleoceras* sp.).
Arieticeras cf. *ruthenense* (Reynès). Thomson and Smith, 1992, p. 37, pl. 15, figs. 1, 2.

Description.—An evolute form with an elliptical to subquadrate whorl section bearing a high keel bordered by flat smooth areas or weak sulci. Ribbing is fairly coarse and densely spaced. Ribs arise near the umbilical shoulder, are rectiradiate in trend and project onto the venter where they fade rapidly.

Type material.—Holotype: Reynès, 1868, pl. 2, fig. 4.

Material.—Six specimens in calcareous sandstone of the upper Fannin Formation.

Measurements.—See Table 32.

Discussion.—The species *A. ruthenense* shows considerable variation in its whorl shape and ornamen-

Table 32.—Measurements of *Arieticeras* cf. *ruthenense* (Reynès, 1868). All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*PRHW*
GSC 98723	35.5	34	12.5	36.8	c9.5	c27.9	13.5	39.7	c70.4	c15
GSC 98724	30	28.5	10.5	36.8	—	26.2	10.4	36.5	—	17

Table 33.—Measurements of *Leptaleoceras* aff. *accuratum* (Fucini, 1931). All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WH*	*WHD*	*PR-HW*
GSC 98593	c55	40	17	42.5	c13	32.5	21
GSC 98599	c47	45	29	44.4	14	31.1	23
GSC 95577	c33	30	11.4	38	12	40	22

Table 34.—Measurements of *Leptaleoceras compressum* (Monestier, 1934). All measurements are in mm.

specimen no.	*DM-AX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WW-WH*	*PR-HW*
GSC 98601	28.5	25	11	44	6.2	24.8	8.2	32.8	75.6	21

tation (Meister, 1989); the poorly preserved Queen Charlotte Islands material compares well with the densely ribbed varieties.

Occurrence.—*A. ruthenense* is a widely distributed Tethyan species reported from the circum-Mediterranean area (Wiedenmayer, 1977; Meister, 1989), British Columbia, and Oregon (Thomson and Smith, 1992). It characterizes the Upper Pliensbachian.

Localities.—I06, I14.

Age.—Kunae Zone (Late Pliensbachian).

Genus **LEPTALEOCERAS** Buckman, 1918

Naxeniceras Fucini, 1931, p. 147.
Distefania Fucini, 1931, p. 153.
Trinacrioceras Fucini, 1931, p. 157.
Seguentia Fucini, 1931, p. 122.
Ugdulenia Cantaluppi, 1970, p. 40.

Type species.—*Leptaleoceras leptum* Buckman, 1918, p. 284, pl. 26, figs. 1–3 by original designation.

Remarks.—Moderately evolute forms with a compressed oval whorl section bearing a keel flanked by smooth bands or sulci. Ribbing is dense and often sinuous. Detailed treatments of the genus are given by Wiedenmayer (1977) and Braga (1983).

Age and distribution.—Most species of this genus occur in the circum-Mediterranean area of the Tethyan Realm ranging through beds that correlate with the upper Margaritatus and Spinatum zones. Occurrences are also known in the northwest European Province, where the genus was first recognized (Buckman, 1918), Oregon (Imlay, 1968), British Columbia (Thomson and Smith, 1992), and Mexico (Erben, 1954). The genus is also questionably present in Argentina amongst material described as *Bouleiceras* sp. (Hillebrandt, 1973b), as discussed by Wiedenmayer (1980, p. 137).

Leptaleoceras aff. **accuratum** (Fucini, 1931)
Plate 22, figures 6, 8, 9

aff. *Arieticeras(?) accuratum* Fucini, 1931, p. 117, pl. 24, fig. 10.
Leptaleoceras pseudoradians (Reynès). Frebold, 1964a, p. 15, pl. 4; 1970, p. 443, pl. 2, fig. 2.
Leptaleoceras cf. *pseudoradians* (Reynès). Imlay, 1981, p. 40, pl. 11, figs. 12, 13.
Arieticeras cf. *domarense* (Meneghini). Imlay, 1981, p. 39, pl. 10, fig. 15 only.
Leptaleoceras accuratum (Fucini) morphotype "*preaccuratum*". Braga, 1983, p. 256, pl. 11, figs. 27–30, pl. 12, figs. 1, 2.
Leptaleoceras aff. *accuratum* (Fucini). Smith, Tipper, Taylor, and Guex, 1988, pl. 4, fig. 9; Thomson and Smith, 1992, p. 34, pl. 13, figs. 1–6.

Description.—Evolute with a compressed, ogival whorl section bearing a keel flanked by smooth areas or weak sulci at large diameters. Ribbing characteristically changes with growth. The nucleus is smooth; the middle whorls (up to umbilical diameters of approximately 15 mm) bear densely spaced, wiry, rectiradiate to gently rursiradiate ribs that project onto the venter; ribs on outer whorls are coarser, less densely spaced and slightly sinuous.

Type material.—Holotype: Fucini, 1931, pl. 8, fig. 10.

Material.—Twelve specimens, mostly external molds, in buff coloured sandstone of the upper Fannin Formation.

Measurements.—See Table 33.

Discussion.—This species is placed in *Leptaleoceras* rather than *Arieticeras* because of its very dense, sharp ribbing. The species is probably closely related to the densely ribbed *A. ruthenense* which is known from the Spatsizi area of north-central British Columbia (Thomson and Smith, 1992) as well as the Queen Charlotte Islands.

Occurrence.—*Leptaleoceras accuratum* is a circum-Mediterranean Tethyan species known from the Upper Pliensbachian of Italy, southern France, Spain, and southern Switzerland (Fucini, 1931; Wiedenmayer, 1980; Braga, 1983). It is also known from the Kunae Zone of North America as discussed by Thomson and Smith (1992).

Localities.—I17.

Age.—Kunae Zone (Late Pliensbachian).

Leptaleoceras compressum (Monestier, 1934)
Plate 22, figure 10

Arieticeras compressum Monestier, 1934, p. 51, pl. 8, figs. 21–23.
Arieticeras compressum var. *semilaevis* Monestier, 1934, p. 51, pl. 8, fig. 20.
non *Fuciniceras compressum* (Monestier). Fischer, 1975, p. 74, pl. 2, fig. 13, 14 (=*Leptaleoceras macrum*).
Fuciniceras aff. *compressum* (Monestier). Fischer, 1975, p. 76, pl. 2, fig. 15.
Leptaleoceras (Leptaleoceras) compressum (Monestier). Wiedenmayer, 1980, p. 118, pl. 22, figs. 6, 9.

Description.—Evolute, slowly expanding form bearing a low keel. The umbilical wall is low and steep, the

Table 35.—Measurements of *Leptaleoceras* sp. All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*PRHW*
GSC 98602	c19	c17	c6	35.3	c4.3	25.3	6.5	38.2	66.2	c23
GSC 98604	25	25	9	36	6.3	25.2	9.3	37.2	67.7	22
GSC 99021	19	19	6.3	33.2	—	—	c7.5	39.5	—	c19
	—	—	3.5	—	3.3	—	5	—	66	—

flanks flat and the venter broadly arched giving an ogival whorl section. The densely spaced, narrow ribs are rectiradiate to gently rursiradiate and projected onto the venter. The whorls are smooth to an umbilical diameter of approximately 5 mm.

Type material.—Syntypes: Monestier, 1934, pl. 8, figs. 21–23.

Material.—One specimen from sandstone of the Fannin Formation.

Measurements.—See Table 34.

Discussion.—This species is included in the genus *Leptaleoceras* rather than *Arieticeras* because of its fine, dense ribbing. *L. compressum* differs from *L.* sp. with which it co-occurs in the Queen Charlotte Islands, by its smaller expansion rate (less than 2 compared to greater than 2), slightly coarser ribbing and its less sharp keel. The slowly expanding *L. macrum* (Monestier, 1934) which Meister (1989; under the generic name *Arieticeras*) considers a synonym of *L. compressum*, differs only in its finer, denser ribbing which arises early in ontogeny, contrasting with the larger, smooth nucleus of *L. compressum.*

Occurrence.—*L. compressum* is known from the Margaritatus Zone of southern France, southern Germany, and southern Switzerland (Monestier, 1934; Fischer, 1975; Wiedenmayer, 1980).

Locality.—I06.

Age.—Kunae Zone (Late Pliensbachian).

Leptaleoceras sp.

Plate 22, figures 7, 11–13
Text-figures 37e-f, 38m

Description.—Midvolute to evolute form with a compressed whorl section bearing a sharp keel. The ribs are fine, densely spaced and gently sinuous. At umbilical diameters greater than approximately 8 mm, the convex flanks flatten slightly and the ornamentation coarsens.

Material.—Twenty-two specimens in calcareous sandstone of the upper Fannin Formation.

Measurements.—See Table 35.

Discussion.—As noted above, *Leptaleoceras compressum* is more coarsely ribbed and slightly more evolute than *L.* sp. It is conceivable that all the specimens represent variants of the same species but *L.* sp. is much more common.

Localities.—DT1, D20, D23, FT2, F11(?), I06, I14.

Age.—Kunae Zone (Late Pliensbachian).

Genus **FONTANELLICERAS** Fucini, 1931

Type species.—*Harpoceras fontanellense* Gemmellaro, 1886 (p. 118, pl. 2, figs. 1, 2) by subsequent designation (Vecchia, 1949, p. 142). The type material has been refigured by Fucini (1931, pl. 24, figs. 21, 22).

Remarks.—Evolute, slowly expanding and stout whorled forms with sulcate keels and strong, simple ribs.

Age and distribution.—A Tethyan form known from the Upper Pliensbachian and lowermost Toarcian of Italy (Fucini, 1931; Cantaluppi and Brambilla, 1968; Fantini Sestini, 1977), southern Switzerland (Wiedenmayer, 1980), Spain (Braga, Jiminéz and Rivas, 1982; Braga, 1983), France (Monestier, 1934), Morocco (Guex, 1973), Japan (Hirano, 1971), and the United States (Imlay, 1968, 1981).

Fontanelliceras sp.

Plate 22, figures 1, 2

Description.—Evolute, slowly expanding form with a slightly compressed whorl section with convex flanks. The venter bears a prominent, weakly sulcate keel. Ribs are simple and coarse; they are rectiradiate to slightly rursiradiate on the flanks and project weakly onto the venter.

Material.—Two internal molds and several fragments preserved in calcareous sandstone of the Fannin Formation.

Measurements.—See Table 36.

Discussion.—These specimens show a resemblance to some forms collected from Alaska and figured under the name of *Fontanelliceras* cf. *fontanellense* by Imlay (1981, pl. 11, figs. 19 and 20). The remainder of Imlay's *F.* cf. *fontanellense* (1981, pl. 11, figs. 17, 18, 21–23) together with *Arnioceras?* sp. indet. of Frebold (1964a) appears to belong to *F. juliae* of Fucini (1931, pl. 8, figs. 28–31). The Queen Charlotte Islands specimens differ from *F. fontanellense* in being more compressed, more weakly sulcate and more coarsely ribbed.

Localities.—D20, D22, E52, I14.

Age.—Kunae Zone (Late Pliensbachian).

Table 36.—Measurements of *Fontanelliceras* sp. All measurements are in mm.

specimen no.	*D*	*UD*	*U*	*WW*	*WH*	*WW-WH*	*PR-HW*
GSC 98583	24	12	50	—	—	—	10
	—	8	—	4.7	5.2	90.4	—

Genus **CANAVARIA** Gemmellaro, 1886

Type species.—Harpoceras (Dumortieria) haugi Gemmellaro, 1886, pl. 1, figs. 1–3 by subsequent designation (Howarth, 1955, p. 167).

Remarks.—Evolute, slowly expanding forms with a subrectangular whorl section. A keel is present flanked by smooth areas or weak sulci. The ribbing is simple, straight to weakly sinuous, with tubercules on the ventral ends. This genus is closely related to the non-tuberculate *Emaciaticeras* and the bituberculate *Tauromeniceras* both of which have been included as subgenera of *Canavaria* by some workers (Wiedenmayer, 1980; Braga, 1983).

Age and distribution.—Canavaria is a circum-Mediterranean form characteristic of the upper part of the Pliensbachian (the Emaciatum Zone in Spain [Braga, 1983] and upper Spinatum Zone equivalents). Material from Oregon referred to *Canavaria* by Imlay (1968) has subsequently been referred to the genus *Oregonites* (Wiedenmayer, 1980) which resembles *Fontanelliceras* except for the irregularity of the ornamentation. *Canavaria* is questionably present in the Spatsizi area of northern British Columbia (Thomson and Smith, 1992).

Canavaria? sp.
Plate 21, figure 5

Description.—An evolute (U=c60) slowly expanding form bearing a sulcate keel. The coarse ribs, which reach a density of approximately 23 per half whorl on the outer whorl, are simple and rursiradiate with their ventral ends swollen. Poorly preserved traces of the septal suture are evident up to the last half whorl.

Material.—One compressed and slightly distorted internal mold preserved in noncalcareous sandstone of the Fannin Formation.

Discussion.—This isolated specimen was collected from an outcrop in an otherwise covered stratigraphic interval on Maude Island situated between sandstones yielding a Carlottense Zone fauna and sandstones yielding a Kunae Zone fauna. The specimen does show the important morphological features of the genus but its poor preservation, the uncertainty of its stratigraphic position, and the fact that this genus is not unequivocally known from any other locality in North America all leave room for doubt as to its true affinity.

Table 37.—Measurements of *Oregonites? dawsoni,* new species. All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WW-WH*	*PR-HW*
GSC 98727	c25	c25	8.8	35.2	7.3	29.2	8	32	91.3	11

Occurrence.—This specimen occurred in sandstones lithologically similar and geographically fairly close to those yielding a Carlottense Zone fauna. There is no associated fauna, however, to confirm this assignment.

Locality.—E61.

Age.—Probably Late Pliensbachian.

Genus **OREGONITES** Wiedenmayer, 1980

Type species.—Oregonites imlayi Wiedenmayer, 1980=*Canavaria* cf. *C. morosa* of Imlay, 1968, p. 35, pl. 5, figs. 12–14 (Wiedenmayer, 1980, p. 124).

Remarks.—Evolute with depressed whorl sections bearing a keel that is simple or flanked either by smooth areas or narrow sulci. Ribs are strong, rursiradiate, sometimes irregularly paired near the umbilical margin. Species of *Fontanelliceras* are more evolute and more regularly ribbed; species of *Arieticeras* have simpler, more rectiradiate ornamentation and whorls that in most cases are more compressed. Many of the species Wiedenmayer (1980) tentatively assigned to *Oregonites,* however, are better accommodated in these genera. The exceptions are Imlay's (1968) species *Fuciniceras* sp. A, *F.* sp. B, *F.* cf. *capellinii,* and *F.* cf. *inclytum.*

Age and distribution.—From the Upper Pliensbachian of North America.

Oregonites? dawsoni, new species
Plate 20, figure 13

Description.—Midvolute, slightly compressed form with an arched venter bearing a sharp keel that is simple where the shell is preserved but flanked by incipient sulci on the internal mold. The specimen is incomplete but the outer half whorl is non-septate and the last quarter whorl shows a decline in the ornament and strength of the keel. The inclined umbilical wall rounds evenly into the gently convex flanks.

The ribs arise near the umbilical shoulder and are strongest on the flanks where they arch backward. The ribs project onto the venter from the ventro-lateral area but they fade and rapidly disappear.

Type material.—Holotype: GSC 98727 (Pl. 20, fig. 13). Preserved in calcareous sandstone of the upper Fannin Formation.

Measurements.—See Table 37.

Derivation of name.—After G.M. Dawson, a pioneer

Canadian geologist who undertook reconnaissance work in the Queen Charlotte Islands during the 19th century.

Discussion.—The stout whorl shape compared with other Pliensbachian hildoceratids, the markedly rursiradiate ribs and the distinct keel are characteristic of the genus *Oregonites* but the assignment to this genus is tentative because the specimen is more involute, more compressed and more regularly ribbed than the forms normally accommodated within *Oregonites*. It is most similar to *Fuciniceras* sp. B, an as yet unnamed species from Oregon described by Imlay (1968) and assigned to *Oregonites* by Wiedenmayer (1980). It differs by having a more compressed whorl section, a more arched venter and ribs that disappear at the ventro-lateral area. In an earlier work (Smith *et al.*, 1988), *O.? dawsoni* was provisionally compared to *"Grammoceras" sygma* Monestier (1934) and assigned to *Fieldingiceras* but Monestier's material from the Margaritatus Zone does not have the distinct keel of *O.? dawsoni.*

Occurrence.—*O.? dawsoni* is unfortunately only known from this single specimen from the Queen Charlotte Islands.

Locality.—E63.

Age.—Carlottense Zone (Late Pliensbachian).

Subfamily **HARPOCERATINAE** Neumayr, 1875

Genus **FIELDINGICERAS** Wiedenmayer, 1980

Fieldingia Cantaluppi, 1970, p. 41.
Grammoceratoides Mattei, 1967, p. 556.

Type species.—*Ammonites fieldingii* Reynès, 1868, p. 97, pl. 4, fig. 1.

Remarks.—Evolute compressed forms that are fairly small and have a sharp keel. Meister (1986) has suggested that *Fieldingiceras* might represent microconchs of *Protogrammoceras*. Smooth and irregularly ribbed forms are known and some workers hold that the costate *F. fieldingii* and the smooth *F. pseudofieldingii* are variants of the same species (Imlay, 1968; Braga, 1983). They are kept separate here because they do not always co-occur at the same locality or within the same geographic area.

This genus was first called *Fieldingia* by Cantaluppi (1970) but Wiedenmayer (1980, p. 128) pointed out that this name is a junior homonym of the hexactinellid sponge *Fieldingia* Kent (1870). Rather than giving Cantaluppi the opportunity to select a new name, Wiedenmayer (1980) simply renamed Cantaluppi's genus *Fieldingiceras*.

Age and distribution.—Characteristic of the Margaritatus Zone of the circum-Mediterranean area. In North America, *Fieldingiceras* is presently known from northern British Columbia and eastern Oregon. Frebold (1964a) figured a ribbed form (Ammonite gen. and sp. indet. 2, pl. 2, fig. 10) from the Telegraph Creek area, British Columbia, that is similar to, if not conspecific with, *Fieldingiceras morganense* reported from the Nicely Formation of eastern Oregon by Imlay (1968). Imlay also recorded a single specimen from the Nicely Formation tentatively assigned to *F. pseudofieldingii.*

Fieldingiceras fieldingii (Reynès, 1868)
Plate 20, figure 14; Plate 21, figure 3;
Text-figure 37c

Ammonites Fieldingii Reynès, 1868, p. 97, pl. 4, fig. 1.
Harpoceras? Fieldingii Reynès. Fucini, 1901a, p. 51, pl. 7, fig. 8.
Grammoceras Fieldingii (Reynès). Monestier, 1934, p. 33, pl. 4, figs. 30, 38, 39 only.
Leptaleoceras (Fieldingia) fieldingii (Reynès). Wiedenmayer, 1980, p. 123, pl. 23, figs. 29, 30.
aff. *Fieldingia* aff. *fieldingii* (Reynès). Mouterde and Rocha, 1981, p. 218, pl. 2, figs. 3–6.
Fieldingiceras fieldingii (Reynès). Braga, 1983, p. 181, pl. 7, figs. 3, 4, 6–11; Meister, 1986, pl. 22, fig. 4.
Fieldingiceras gr. *fieldingii* (Reynès). Dommergues, Ferretti, Géczy, and Mouterde, 1983, p. 479, pl. 2, figs. 15–20.
Protogrammoceras (Fieldingiceras) fieldingii (Reynès). Meister, 1989, p. 40, pl. 4, figs. 2, 3, 5.

Description.—Midvolute, with a compressed whorl section bearing a pronounced, simple keel. The outer half whorl of specimen GSC 98728 is non-septate, egresses and shows a weakening of the keel and ornamentation. The last few ribs are approximated and the peristome flares slightly and projects ventrally. These features indicate that this form is mature.

The ribs arise near the umbilical shoulder, are rursiradiate on the flanks and project onto the venter where they fade rapidly. On the outer quarter whorl of specimen GSC 98728, weak ribs can be seen in oblique light projecting forward strongly onto and over the venter where the keel is weakening.

Type material.—Holotype: Reynès, 1868, pl. 4, fig. 1.

Material.—Two specimens in sandstone of the upper Fannin Formation.

Measurements.—See Table 38.

Occurrence.—From the Margaritatus Zone of Italy (Fucini, 1904; Dommergues *et al.*, 1983), southern France (Monestier, 1934), southern Switzerland (Wiedenmayer, 1980), and Spain (Braga, 1983).

Locality.—ET5.

Age.—Not in place but originating from the Carlottense Zone (Late Pliensbachian).

Fieldingiceras pseudofieldingii (Fucini, 1904)
Plate 21, figures 1, 4; Plate 22, figures 3–5
Text-figures 37g, 38n

Harpoceras(?) pseudofieldingii Fucini, 1904, p. 251, pl. 41, fig. 4.

Table 38.—Measurements of *Fieldingiceras fieldingii* (Reynès, 1868). All measurements are in mm.

specimen no.	*DMAX*	*DPHRAG*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*PRHW*
GSC 98728	19	c14	19	6.5	34.2	5.5	28.9	6.5	34.2	84.6	10

Praeleioceras pseudofieldingii (Fucini). Fucini, 1931, p. 108, pl. 22, figs. 12, 13.
Grammoceras penenudum Monestier, 1934, p. 41, pl. 4, figs. 9–16; pl. 8, figs. 28, 29.
Grammoceras intermediate between *fieldingii* and *pseudofieldingii* Monestier, 1934, p. 36, pl. 4, figs. 22, 23.
Grammoceras pseudofieldingii (Fucini). Monestier, 1934, p. 35, pl. 4, figs. 24–26.
Protogrammoceras? cf. *P.? pseudofieldingi* (Fucini). Imlay, 1968, p. C40, pl. 7, figs. 5–7.
Leptaleoceras (Fieldingia) pseudofieldingi (Fucini). Wiedenmayer, 1980, p. 123, pl. 23, fig. 31.
Fieldingiceras fieldingii (Fucini). Braga, 1983, p. 181, pl. 7, fig. 5 only.

Description.—Evolute with a compressed whorl section bearing a sharp keel on an arched venter. The umbilical wall is low and steep and the flanks flat. The shell is smooth except for barely visible, radially arranged and ventrally projected striations.

Type material.—Holotype: Fucini, 1904, pl. 41, fig. 4.

Material.—Six specimens preserved in calcareous sandstone of the upper Fannin Formation.

Measurements.—See Table 39.

Discussion.—This form differs from the nuclei of associated species of *Arieticeras* by its compressed whorls and lack of ornamentation to relatively large shell diameters.

Occurrence.—In western Europe *Fieldingiceras pseudofieldingii* is a Tethyan species known from Italy (Fucini, 1904), southern France (Monestier, 1934), southern Switzerland (Wiedenmayer, 1980), and Spain (Braga, 1983) where it characterizes the lower Margaritatus Zone and its equivalents.

Localities.—D19, D20, FT2, I06, I07.

Age.—Kunae Zone (Late Pliensbachian).

Genus **FUCINICERAS** Haas, 1913

Eofuciniceras Cantaluppi, 1970, p. 41.
Neofuciniceras Cantaluppi, 1970, p. 41.

Type species.—*Harpoceras lavinianum* Meneghini *in* Fucini, 1900, pl. 11, figs. 6 and 7, by original designation (Haas, 1913, p. 75).

Table 39.—Measurements of *Fieldingiceras pseudofieldingii* (Fucini, 1904). All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WW-WH*
GSC 98587	c24	17 1	6.5	38.2	—	—	6.5	38.2	—
GSC 98590	15.4	14.8	5.7	38.5	3.8	25.7	5.8	39.2	65.5
GSC 99018	13.8	13.4	4.6	34.3	3.5	26.1	5.2	38.8	67.3

Remarks.—When Spath (1913) first recognized the genus *Protogrammoceras* he included a group whose ribs did not project onto the venter as was typical of *Protogrammoceras.* Unbeknownst to Spath, this group had been independently recognized by Haas (1913) and named *Fuciniceras. Fuciniceras* may also be distinguished from *Protogrammoceras* by its less sinuous ribbing which is rursiradiate on the upper flank and the tendency to have a flat, bisulcate venter; otherwise the genera are very similar and obviously closely related.

Age and distribution.—As with *Protogrammoceras, Fuciniceras* is widely distributed but most abundant and diverse in the Tethyan Realm. It is restricted to the Pliensbachian, ranging from the upper Ibex Zone into the Margaritatus Zone (Géczy, 1976; Wiedenmayer, 1977, 1980; Meister, 1986).

Fuciniceras cf. **targionii** (Fucini, 1905)
Plate 22, figures 14, 15

cf. *Hildoceras Targionii* Fucini, 1905, p. 271, pl. 44, fig. 1.
Fuciniceras cf. *targionii* (Fucini). Wiedenmayer, 1980, p. 85, pl. 11, figs. 6, 7.

Description.—Midvolute, moderately slowly expanding form with what appears to have been a subquadrate, compressed whorl section. The umbilical wall is high and rounds rapidly into the flat flanks. The venter bears a pronounced, sulcate keel. The nucleus of GSC 98606 (Pl. 22, fig. 14) appears to be smooth but the ribbing on the rest of the whorls is weak on the lower flank becoming increasingly stronger and rursiradiate on the upper flank. The sinuous trace of a former aperture followed by subdued ornamentation is evident in specimen GSC 98609 (Pl. 22, fig. 15).

Type material.—Holotype: Fucini, 1905, pl. 44, fig. 1.

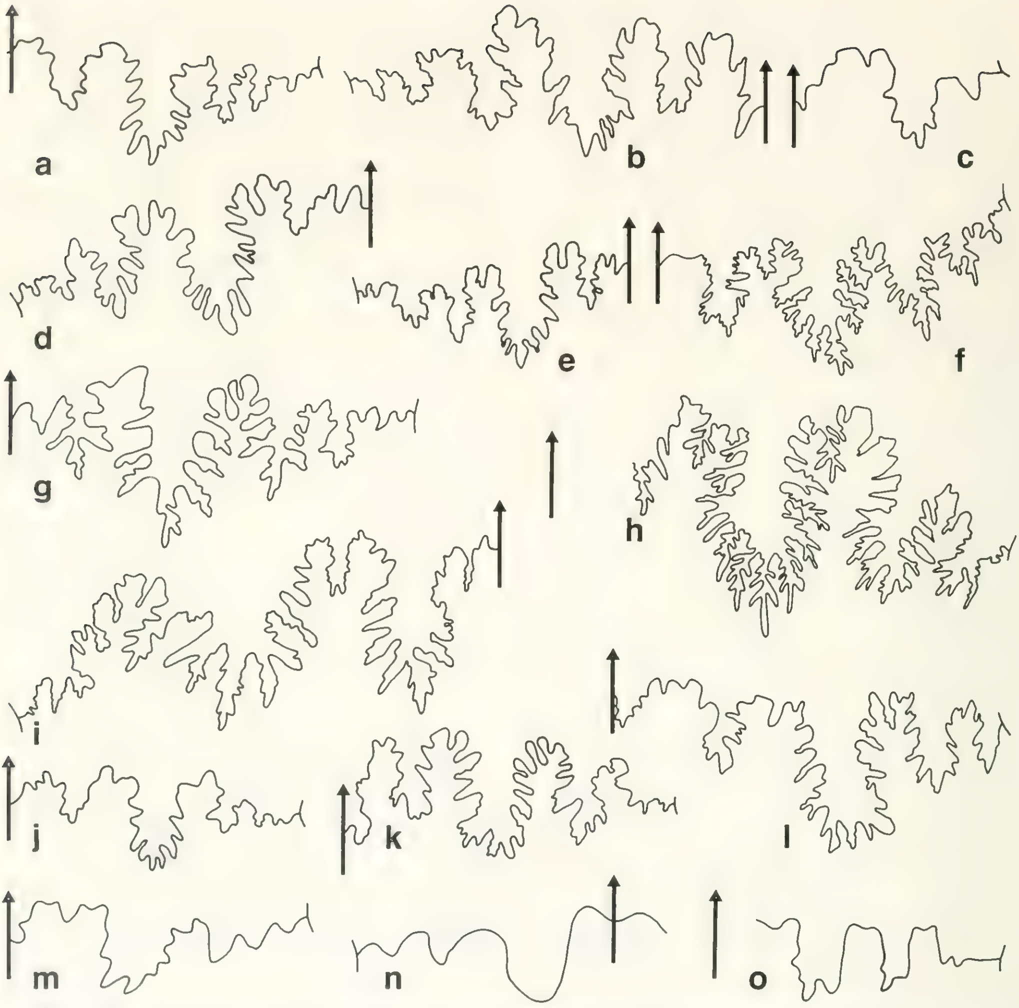
Material.—Two poorly preserved, partial internal molds in siltstone of the Fannin Formation.

Discussion.—The distinctive ornamentation of the Queen Charlotte Islands material compares well with the figured material of *F. targionii.* The ventral features and whorl shape also appear to correspond, as far as preservation permits comparison.

Occurrence.—*F. targionii* occurs in Italy (Fucini, 1905) and the Davoei Zone of Switzerland (Wiedenmayer, 1980).

Locality.—I17.

Age.—Kunae Zone (Late Pliensbachian).



Text-figure 38.—Traces of the septal suture for species of the Hildoceratidae at whorl heights (WH) indicated. a. *Lioceratoides (Pacificeras) propinquum* (Whiteaves, 1884) (GSC 87806, WH = 11 mm); b. *Protogrammoceras (Protogrammoceras) aequiondulatum* (Bettoni, 1900) (GSC 98649, WH = 14.3 mm); c. *Fuciniceras* aff. *intumescens* (Fucini, 1901) (GSC 87801, WH = 6.2 mm); d-g. *Lioceratoides (Pacificeras) propinquum* (Whiteaves, 1884) (d. GSC 98690, WH = 5.2 mm, e. GSC 98685, WH = 10.7 mm, f. GSC 98687, WH = 17.6 mm, g. GSC 87804, WH = 15.2 mm); h. genus and species indet. (GSC 99013, WH = 41.1 mm); i. *Protogrammoceras (Protogrammoceras) skidegatense*, n. sp. (Paratype GSC 98741, WH = 49.8 mm); j. *Protogrammoceras (Protogrammoceras)*? sp. (GSC 98744, WH = 7.9 mm); k,l. *Protogrammoceras (Protogrammoceras)* cf. *paltum* (Buckman, 1922) (k. GSC 99017, WH = 11.1 mm, l. GSC 99015, WH = 20.9 mm); m. *Leptaleoceras* sp. (GSC 98602, WH = 4.5 mm); n. *Fieldingiceras pseudofieldingii* (Fucini, 1904) (GSC 98590, WH 3.3. mm); o. *Arieticeras disputabile* (Fucini, 1908) (GSC 98719, WH = 4 mm).

Fuciniceras aff. **intumescens**
(Fucini, 1901)
Plate 22, figure 16, Text-figure 39j

aff. *Hildoceras intumescens* Fucini, 1901a, p. 89, pl. 13, fig. 3; 1905, p. 271, pl. 43, fig. 15.
aff. *Fuciniceras? intumescens* (Fucini). Venzo, 1952, pl. A, fig. 3.
non *Arieticeras intumescens* (Fucini). Cantaluppi and Savi, 1968, p. 246, pl. 21, fig. 6.
Fuciniceras? cf. *intumescens* (Fucini). Imlay, 1968, p. C42, pl. 8, figs. 1–7, 9, 10.
Fuciniceras aff. *intumescens* (Fucini). Smith, Tipper, Taylor, and Guex, 1988, pl. 4, fig. 14.

Description.—Evolute, slowly expanding shell with a compressed, elliptical whorl section bearing a simple keel. The ribs project forward on the lower part of the flank and then trend more rursiradiately on the upper flank; they are only weakly projected onto the venter where they quickly fade.

Type material.—Holotype of *Fuciniceras intumescens*: Fucini, 1901a, pl. 13, fig. 3.

Material.—Eight specimens from the upper sandstone of the Fannin Formation.

Discussion.—This material is reminiscent of specimens collected from the Nicely Formation in Oregon and compared with *F. intumescens* by Imlay (1968). The type specimen of *F. intumescens* is less compressed.

Occurrence.—*F. intumescens* is known from the Upper Pliensbachian of Italy. *F.* aff. *intumescens* is reported from the Upper Pliensbachian of Oregon (Imlay, 1968).

Localities.—E52, E60, I06.

Age.—Kunae Zone (Late Pliensbachian).

Fuciniceras sp.
Plate 21, figures 6, 7

Description.—These midvolute specimens have a compressed whorl section. The steep umbilical wall rounds quickly into the flanks that are subparallel in their lower and middle parts and thereafter convergent towards the venter. On the smaller specimen (Pl. 21, fig. 7) the prominent keel is bordered by incipient sulci. The larger specimen has a less well preserved venter but the keel was evidently flanked by deep sulci producing an almost tricarinate effect.

The ribs are coarse. They are weakest near the umbilicus where they are gently prorsiradiate but increase in strength near the mid-flank where there is an inflection. The ribs trend rursiradiately across the upper flank (markedly in the larger specimen figured on Plate 21, fig. 6) and begin to project toward the venter but terminate against the sulci.

Material.—Two incomplete specimens originating from the sandstones of the Fannin Formation.

Discussion.—These fragments are assigned to *Fuciniceras* because of the backward inflection of the ribs on the upper flank and the presence of a sulcate keel. Their strong ribs are reminiscent of species such as *Fuciniceras targionii* (Fucini) and *F. lavinianum* (Fucini).

Locality.—FT2.

Age.—Associated with ammonites of the Kunae Zone (Late Pliensbachian).

Genus **PROTOGRAMMOCERAS** Spath, 1913
Subgenus **PROTOGRAMMOCERAS** Spath, 1913

Wrightia Gemmellaro, 1886, p. 190.
Paltarpites Buckman, 1922, pl. 362A.
Argutarpites Buckman, 1923, pl. 363.
Bassaniceras Fucini, 1929, p. 63.
Eoprotogrammoceras Cantaluppi, 1970, p. 42.
Neoprotogrammoceras Cantaluppi, 1970, p. 42.

Type species.—*Grammoceras bassanii* Fucini, 1901a, p. 72, pl. 10, fig. 6 by subsequent designation (Spath, 1919, p. 547). The type material has been refigured by Cantaluppi (1972).

Remarks.—Midvolute forms with an ogival or compressed elliptical whorl section and a strongly carinate venter that is sometimes bisulcate. Ribs are sinuous and projected onto the venter. We agree with Howarth (1973) who points out that there is no difference between the type material of *Protogrammoceras* and *Paltarpites* worthy of generic distinction.

Age and distribution.—*Protogrammoceras (Protogrammoceras)* has a wide distribution but is at its most abundant and diverse in the circum-Mediterranean area within the Tethyan Realm. It ranges from the Lower Pliensbachian (Ibex Zone) to the basal Toarcian.

Protogrammoceras (Protogrammoceras)
aequiondulatum (Bettoni, 1900)
Plate 24, figures 7–9; Text-figures 38b, 39f,t

Harpoceras? aequiondulatum Bettoni, 1900, p. 67, pl. 6, fig. 11.
Grammoceras aequiondulatum Bettoni. Del Campana, 1900, p. 625, pl. 8, fig. 32.
Harpoceras aequiondulatum Bettoni. Fucini, 1908b, p. 39, pl. 2, figs. 46, 47.
Harpoceras percostatum Fucini, 1908b, p. 37, pl. 1, fig. 29.
Protogrammoceras aequiondulatum (Bettoni). Fucini, 1924, p. 61, pl. 7, figs. 12; Wiedenmayer, 1980, p. 85, pl. 11, figs. 8, 9; Braga, 1983, p. 161, pl. 5, figs. 3–5.
Protogrammoceras? percostatum (Fucini). Fucini, 1924, p. 57, pl. 8, fig. 1.
Neoprotogrammoceras aequiondulatum (Bettoni). Ferretti, 1972, p. 116, pl. 15, fig. 3.
(?)*Argutarpites* cf. *Aequiondulatum* (Bettoni). Dubar and Mouterde, 1978, p. 63.
Protogrammoceras percostatum (Fucini). Wiedenmayer, 1980, p. 88, pl. 12, figs. 10–12.

Table 40.—Measurements of *Protogrammoceras* (*Protogrammoceras*) *aequiondulatum* (Bettoni, 1900). All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*PRHW*
GSC 98649	—	—	c21	—	25	—	47	—	53.2	—
	—	—	8	—	—	—	—	—	—	23
GSC 98734	c42	35	10	28.6	c8.5	24.3	15.5	44.3	c54.8	24
GSC 98735	28.5	28.5	18	28.1	7.4	26.0	12.2	42.8	60.7	24

Description.—An involute, rapidly expanding form with compressed whorls. The umbilical wall is low, the flanks flat to weakly convex, and the narrow venter is arched. The ribs are simple, sinuous and strongly projected onto the venter. Rib frequencies are high with a tendency for the ribs to become flat-topped with growth.

Type material.—Holotype: Bettoni, 1900, pl. 6, fig. 11.

Material.—Five specimens and numerous fragments preserved in calcareous sandstone of the upper Fannin Formation.

Measurements.—See Table 40.

Discussion.—Most of the figured specimens of *Protogrammoceras (P.) aequiondulatum* are small, of the diameter of the specimens illustrated as figures 7 and 9 on Plate 24. The larger specimen (Pl. 24, fig. 8) shows that ribbing style changes with growth to resemble the similarly involute species *Protogrammoceras percostatum* which is recognized as a subjective junior synonym by Braga (1983).

P. (P.) aequiondulatum is more involute and rapidly expanding than other species of *Protogrammoceras* found in the Queen Charlotte Islands with the exception of *P. (P.)?* sp. which is more coarsely ribbed.

Occurrence.—*P. (P.) aequiondulatum* is a Tethyan species found in Italy, Spain, and possibly Morocco where it is characteristic of the Upper Pliensbachian (Dubar and Mouterde, 1978; Wiedenmayer, 1980; Braga, 1983).

Localities.—B06, ET5, E62, E63.

Age.—Carlottense Zone (Late Pliensbachian).

Protogrammoceras (Protogrammoceras)? sp.

Plate 23, figures 1–3; Text-figures 38j, 39c

Harpoceras cf. *exaratum* (Young and Bird). Frebold, 1964a, p. 16, pl. 6, fig. 3 only.

Description.—Midvolute to involute, rapidly expanding forms with a compressed whorl section. The umbilical wall rounds rapidly into the gently convex flanks that converge weakly towards the venter that bears a simple, pronounced, blunt keel. Ornamentation is strong throughout growth and falcoid in trend. Where the ribs project onto the venter on some parts of the shell, short and much weaker intercalated ribs are present.

Material.—Three specimens preserved in calcareous sandstone of the upper Fannin Formation.

Measurements.—See Table 41.

Discussion.—These forms possibly belong to the genus *Protogrammoceras* on the basis of the trajectory of their simple ribs. Ribbing is quite strong and although there are parallels, such as in *Protogrammoceras celebratum,* the Queen Charlotte material is notably more involute.

Localities.—ET5, E62, E63.

Age.—Carlottense Zone (Late Pliensbachian).

Protogrammoceras (Protogrammoceras) kurrianum (Oppel, 1862)

Plate 24, figures 5, 6; Text-figure 39g

Ammonites kurrianus Oppel, 1862, p. 136, pl. 42, fig. 3; Quenstedt, 1883, p. 421, pl. 53, fig. 12.

Argutarpites argutus Buckman, 1923, pl. 363.

Harpoceras densecapillatum Fucini, 1924, p. 53, pl. 6, figs. 12, 13.

Polyplectus kurrianus (Oppel). Monestier, 1934, p. 90, pl. 5, figs. 12, 23; pl. 10, figs. 1, 17; pl. 11, figs. 3, 22.

Paltarpites cf. *argutus* (Buckman). Imlay, 1968, p. 37, pl. 5, figs. 20–22, 24, 25.

Paltarpites argutus (Buckman). Frebold, 1970, p. 444, pl. 4, figs. 8–10; Hillebrandt, 1987, pl. 5, fig. 2.

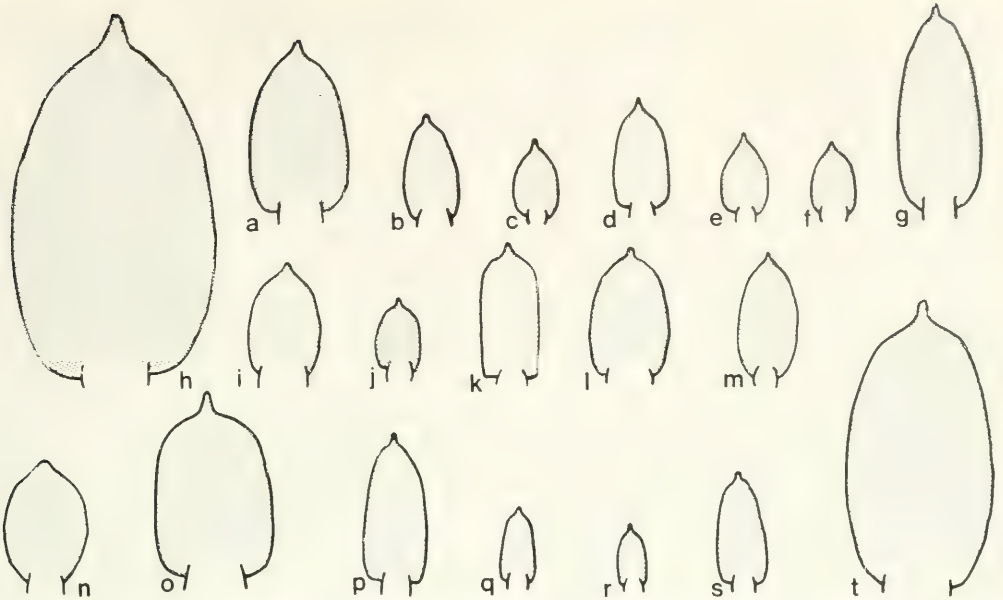
Protogrammoceras cf. *P. argutum* (Buckman). Imlay, 1981, p. 41, pl. 11, fig. 14.

Paltarpites sp. Pérez, 1982, pl. 19, fig. 6.

Protogrammoceras pectinatum (Meneghini, 1881). Smith, Tipper, Taylor, and Guex, 1988, pl. 5, fig. 12.

Table 41.—Measurements of *Protogrammoceras* (*Protogrammoceras*) sp. All measurements are in mm.

specimen no.	*DMAX*	*DPHRAG*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*PRHW*
GSC 98745	26.0	—	26.0	5.7	21.9	7.7	29.6	12.5	48.1	61.6	17
GSC 98744	27.0	—	27.0	6.0	22.2	—	—	12.6	45.2	—	21
GSC 99016	c41.0	—	35.0	9.4	26.9	9.0	25.7	15.0	42.9	60.0	17



Text-figure 39.—Whorl shape cross-sections for species of the Harpoceratinae. Figures are natural size. a,s. *Lioceratoides (Lioceratoides) allifordense* (McLearn, 1930) (a. GSC 98736, s. GSC 98641); b,d,e. *Protogrammoceras (Protogrammoceras)* cf. *paltum* (Buckman, 1922) (b. GSC 99017, d. GSC 98697, e. GSC 98746); c. *Protogrammoceras (Protogrammoceras)*? sp. (GSC 98745); f,t. *Protogrammoceras (Protogrammoceras) aequiondulatum* (Bettoni, 1900) (f. GSC 98735, t. GSC 98649); g. *Protogrammoceras (Protogrammoceras) kurrianum* (Oppel, 1862) (GSC 87808); h. *Protogrammoceras (Protogrammoceras) skidegatense*, n. sp. (Paratype GSC 98739); i. *Protogrammoceras (Matteiceras)* cf. *diornatum* Domergues et al., 1985 (GSC 99014); j. *Fuciniceras* aff. *intumescens* (Fucini, 1901) (GSC 87801); k,o. *Lioceratoides (Pacificeras) angonius* (Fucini, 1931) (k. GSC 98611, o. GSC 98732); l,m. *Tiltoniceras antiquum* (Wright, 1882) (l. GSC 98731, m. GSC 98716); n,q. *Lioceratoides (Pacificeras) propinquum* (Whiteaves, 1884) (n. GSC 87804, q. GSC 87806); p. *Lioceratoides (Lioceratoides) involutum*, n. sp. (Paratype GSC 98644); r. *Lioceratoides* sp. juv. (GSC 98642).

Protogrammoceras (Paltarpites) kurrianus (Oppel, 1862). Meister, 1989, p. 41, pl. 8, figs. 1, 2.

Protogrammoceras (Protogrammoceras) kurrianum (Oppel). Howarth, 1992, p. 60, pl. 3, figs. 2, 3.

Description.—Midvolute form with a compressed whorl section. The umbilical wall is low and the flanks weakly convex, converging towards a narrow venter bearing a high, simple keel. Ornamentation is fine and dense having a flat-topped appearance on most larger whorls. The largest specimen in the collection is incomplete but had an estimated diameter of at least 200 mm. Its last quarter whorl, which is apparently nonseptate, is very weakly and densely ribbed. All ribs have a sinuous trend with a strong projection onto the venter.

Type material.—Holotype: Oppel, 1862, fig. 3. Refigured by Fischer (1975, pl. 2, fig. 5) and Schlegelmilch (1976, pl. 42, fig. 5).

Material.—Six incomplete specimens preserved in calcareous sandstone of the upper Fannin Formation.

Measurements.—See Table 42.

Discussion.—According to Howarth (1992), *P. (P.) kurrianum* is a senior subjective synonym of *P. (P.) argutum* (Buckman) and *P. (P.) densecapillatum* (Fucini). *P. (P.) kurrianum* is more evolute and slowly expanding than other species of *Protogrammoceras* from the Queen Charlotte Islands with the exception of *P. (P.)?* sp. whose ribs are coarser, less densely spaced and strongest on the upper part of the flank.

Occurrence.—*Protogrammoceras (P.) kurrianum* is widely distributed in Europe where it is characteristic of Margaritatus and Spinatum zones. In the Americas it is known from the Upper Pliensbachian of Chile (Pérez, 1982; Hillebrandt, 1987), Oregon (Imlay, 1968), northern British Columbia (Frebold, 1970; Thomson and Smith, 1992), and Alaska (Imlay, 1981).

Table 42.—Measurements of *Protogrammoceras* (*Protogrammoceras*) *kurrianum* (Oppel, 1862). All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*PRHW*
GSC 87808	c90	84	24	28.6	c17	20.2	34.3	40.8	49.6	38
	—	—	15	—	—	—	—	—	—	36
GSC 98733	c73	c70	21.5	30.7	—	—	—	—	—	c44
	—	—	10	—	—	—	—	—	—	23

Localities.—D24, ET5, E67, E68.

Age.—Carlottense Zone (Late Pliensbachian).

Protogrammoceras (Protogrammoceras) cf. **paltum** (Buckman, 1922)

Plate 24, figures 1–4; Text-figures 38k-l, 39b,d,e

cf. *Paltarpites paltus* Buckman, 1922, pl. 362A.

Harpoceras cf. *exaratum* (Young and Bird). Frebold, 1964a, p. 16, pl. 6, figs. 1, 5.

Paltarpites paltus Buckman. Frebold, 1970, p. 443, pl. 4, figs. 5–7.

Protogrammoceras cf. *P. paltum* (Buckman). Imlay, 1981, p. 41, pl. 12, figs. 11, 12.

cf. *Protogrammoceras (P.) paltum* Buckman. Howarth, 1992, p. 57, pl. 1, figs. 1–3; pl. 2, figs. 1,3; Text-figure 11.

Description.–The specimens available are small, incomplete individuals that are midvolute (U=c25) with compressed whorls bearing broad sinuous ribs that project onto the venter where there is a pronounced, simple keel.

Type material.—Holotype: Buckman, 1922, pl. 362A.

Material.—Fourteen specimens preserved in calcareous sandstone of the upper Fannin Formation.

Discussion.—Because of their small size, it is difficult to identify these specimens with confidence. They are similar to other poorly preserved specimens from the Upper Pliensbachian of North America that have been compared with *P. paltum* in the past (Frebold, 1970; Imlay, 1981; Thomson and Smith, 1992).

Occurrence.—*Protogrammoceras (P.) paltum* is widespread in Europe, particularly in the south, where it ranges in age from the Margaritatus Zone into the basal Toarcian (Howarth, 1992). In North America it has been reported from the Upper Pliensbachian of northern British Columbia (Frebold, 1970; Thomson and Smith, 1992), Alaska (Imlay, 1981), and Arctic Canada (Hall and Howarth, 1983). The species has not yet been recorded from the conterminous United States or South America.

Localities.—D24-D27, ET5, E62, E63, E65, E66, I03.

Age.—Carlottense Zone (Late Pliensbachian) to early Toarcian.

Protogrammoceras (Protogrammoceras) skidegatense, new species

Plate 25, figures 1–3; Text-figures 38i, 39h

Paltarpites sp. indet. Sey and Kalacheva, 1980, p. 69, pl. 3, figs. 1, 2(?).

Description.—This species reaches a large size as illustrated in Plate 25, figure 3. The largest specimen in the collection, which is incomplete and almost wholly septate, reaches an estimated shell diameter of 260 mm. The shell is midvolute and rapidly expanding with a compressed whorl section. The umbilical wall is low and rounded, the flanks flat, and the narrow venter bears a prominent keel.

Ornamentation is strongest on the inner whorls where it consists of broad flat-topped to weakly rounded ribs that are prorsiradiate on the lower flank but arch backward on the upper flank; they project strongly onto the venter. At umbilical diameters of about 20 mm, the ribbing weakens, increases in density and is notably flat-topped. Large whorls, which show some indication of egression, are smooth.

Type material.—Holotype: specimen GSC 98740 (Pl. 25, fig. 2). Paratypes: specimens GSC 98739 (Pl. 25, fig. 3) and GSC 98741 (Pl. 25, fig. 1).

Material.—Nine specimens preserved in calcareous sandstone of the upper Fannin Formation.

Measurements.—See Table 43.

Derivation of name.—From Skidegate Inlet, separating Moresby and Graham islands, where the specimens originate.

Discussion.—This species is included in *Protogrammoceras* rather than *Lioceratoides* because its ribbing is consistently simple. The weakness and density of the ribbing on the outer whorls are reminiscent of *Protogrammoceras kurrianum* (a synonym of *P. argutum*) and allied forms which some workers assign to the genus or subgenus *Paltarpites.* The rapidly expanding,

Table 43.—Measurements of *Protogrammoceras* (*Protogrammoceras*) *skidegatense,* new species. All measurements are in mm.

specimen no.	*DMAX*	*UD*	*WW*	*WH*	*WWWH*	*PRHW*
GSC 98739	c190	46	35.3	60.4	58.4	0
	—	28	23	42	54.8	—
	—	9	—	—	—	20
GSC 98740	c125	37	c26.5	c46	57.6	—
	—	14	—	—	—	35
GSC 98741	c135	41	c30	59.4	c50.5	—
	—	17	—	—	—	c26

fairly involute and compressed shell together with the change of ribbing styles during ontogeny, however, set *P. skidegatense* apart from all these species.

Occurrence.—In North America this species is only presently known from the Queen Charlotte Islands where it is restricted to the Carlottense Zone. It is also known from the uppermost Pliensbachian of eastern Russia (Sey and Kalacheva, 1980).

Localities.—D24, D25, E63.

Age.—Carlottense Zone (Late Pliensbachian).

Subgenus **MATTEICERAS** Wiedenmayer, 1980

Type species.—*Ammonites nitescens* Young and Bird, 1828, p. 257 by original designation (Wiedenmayer, 1980, p. 124).

Remarks.—Ribs are coarse and strongest on the middle and upper parts of the flanks where tubercles may develop on the ventro-lateral shoulder. The occurrence of this subgenus in Europe is documented by Wiedenmayer (1980), Dommergues and Mouterde (1980), Dommergues *et al.* (1985), and Howarth (1992).

Age and distribution.—A group originating in Tethys that made early incursions into northwest Europe where endemic species evolved. The subgenus is characteristic of the Margaritatus Zone.

Protogrammoceras (Matteiceras) cf. **diornatum**
Dommergues, Meister and Fauré, 1985
Plate 23, figures 5–7; Text-figure 39i

cf. *Harpoceras volubile* (Fucini). Monestier, 1934, p. 83, pl. 1, figs. 4, 5, 20, 28.

Protogrammoceras gr. *isseli* (Fucini). Dommergues and Mouterde, 1980, pl. 1, figs. 18–20.

Protogrammoceras intermediate between *P. isseli* (Fucini) and *P. monestieri* (Fischer). Dommergues and Mouterde, 1980, pl. 3, figs. 1–3.

cf. *Protogrammoceras (Matteiceras) diornatum* Dommergues, Meister, and Fauré, 1985, p. 159, pl. 1, fig. 2; pl. 2, fig. 2; pl. 3, fig. 1.

Description.—Evolute form (U=c33) with a low expansion rate. The whorls are compressed with a low, steep umbilical wall, flat flanks and a broad venter bearing a pronounced, simple keel. The ribs are only weakly sinuous. They begin part way up the flank, are gently rursiradiate on the upper flank and weakly projected onto the venter where they fade before reaching the keel.

Type material.—Dommergues *et al.*, 1985; Holotype: pl. 2, fig. 2; paratypes: pl. 1, fig. 2, pl. 3, fig. 1.

Material.—Three incomplete specimens preserved in calcareous sandstone of the upper Fannin Formation.

Discussion.—This species differs from all other species of *Protogrammoceras* from the Queen Charlotte Islands by being the most evolute and in having its ornamentation confined to the middle and upper part of the flank.

Detailed studies of the evolution of *Protogrammoceras* based on large samples assembled by Dommergues and Mouterde (1980) and Dommergues *et al.* (1985) indicate an early appearance (Margaritatus Zone) of an eventually stout ribbed group whose ribs trend rursiradiately on the upper flank and often bear tubercles on the ventro-lateral shoulder. These species are accommodated in the subgenus *Matteiceras* (Dommergues *et al.*, 1985); included is the species *Protogrammoceras (M.) monestieri,* thought to be derived from the densely ribbed *Protogrammoceras (P.) isseli.* The three specimens from the Queen Charlotte Islands compare most favorably with forms intermediate between *P. (P.) isseli* and *P. (M.) monestieri* as illustrated by Dommergues and Mouterde (1980). These intermediate forms were subsequently included in the species *P. (Matteiceras) diornatum.* The designated holotype for this species (Dommergues *et al.*, 1985, pl. 2, fig. 2) has developed a strongly sulcate keel and fairly flexuous ribbing but at a shell diameter larger than any of the Queen Charlotte Islands specimens. Because of the discrepancy in size, a more confident species assignment will have to await the collection of larger and better preserved specimens.

Occurrence.—*Protogrammoceras (Matteiceras) diornatum* is known from the Margaritatus Zone of Switzerland, southern France, and Portugal.

Localities.—D20, FT2, I06.

Age.—Kunae Zone (Late Pliensbachian).

Genus and species indet.
Plate 23, figure 4; Text-figure 38h

Description.—A large, completely septate specimen that had a shell diameter in excess of 160 mm. The shell is evolute, expands fairly slowly and has a compressed whorl section (WWWH=c58). The umbilical wall is almost vertical, the umbilical shoulder pronounced and the flanks fairly flat. The arched venter bears a pronounced simple keel.

Ribs arise at the umbilical shoulder where, on most whorls, they merge and are weakly swollen. On the outer half whorl, the ribs fade on the lower part of the flank. Ribs are rectiradiate, gently sinuous on the flank and strongly projected onto the venter.

Material.—One internal mold from the upper Fannin Formation.

Discussion.—This specimen was not found in place but it occurred with many float Kunae Zone ammonites adjacent to in situ material; the possibility of it being derived from elsewhere in the section is considered remote. It could be a species of *Protogrammoceras* except for the fusing and swelling of ribs on the um-

Table 44.—Measurements of *Lioceratoides* (*Lioceratoides*) *allifordense* (McLearn, 1930). All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*
GSC 9053	c76.3	c76.3	23.5	30.8	14.3	18.7	32.3	42.3	44.3
	—	24.1	—	—	c5.0	20.7	11.3	46.8	44.2
GSC 98641	45	45	11.2	24.9	c9.5	21.1	20	44.4	c47.5

bilical shoulder. More material whose stratigraphic position is unequivocal must be collected before the affinities of this form can be properly assessed.

Locality.—FT2.

Age.—Probably from the Kunae Zone.

Genus **LIOCERATOIDES** Spath, 1919

Subgenus **LIOCERATOIDES** Spath, 1919

Platyharpites Buckman, 1927, pl. 698.
Praeleioceras Fucini, 1929, p. 71.
Nagatoceras Matsumoto *in* Matsumoto and Ono, 1947, p. 28.
Neolioceratoides Cantaluppi, 1970, p. 40.

Type species.—*Leioceras? Grecoi* Fucini, 1901a, p. 91, pl. 11, figs. 4, 5, by original designation (Spath, 1919, p. 174).

Remarks.—Species of *Lioceratoides* are keeled, midvolute to involute forms with compressed whorl sections. Ribbing is falcoid or sinuous, sometimes irregular, and on early whorls shows strong primary and weaker secondary ribs; outer whorls may be smooth. See the remarks under *Pacificeras.*

Age and distribution.—*Lioceratoides* is a Tethyan genus most characteristic of the Upper Pliensbachian but it ranges into the Lower Toarcian (Guex, 1973; Wiedenmayer, 1980; Donovan *et al.*, 1981). The genus is also known in southern Japan (Hirano, 1971) and in Russia near Vladivostok (as *Protogrammoceras* cf. *serotinum, in* Sey and Kalacheva, 1980).

Lioceratoides (Lioceratoides) allifordense
(McLearn, 1930)
Plate 26, figures 5, 6, 9–11; Text-figure 39a,s

Harpoceras allifordense McLearn, 1930, p. 4, pl. 2, fig. 1; McLearn, 1932, p. 65, pl. 5, figs. 1–3; Frebold, 1964b, pl. 8, fig. 5 (holotype refigured).

Description.—Midvolute form with compressed whorls bearing a pronounced, flat-topped keel. The umbilical wall is low and steep, the flanks flat, and the venter gently arched.

The innermost whorls bear coarse primary ribs and finer secondary ribs that arise by bifurcation and intercalation. At umbilical diameters greater than approximately 4 mm the complex ribbing gives way to broad flat-topped ribs that are flexuous on the flanks and strongly projected onto the venter. At umbilical diameters greater than approximately 10 mm, the ribs fade and the shell becomes smooth except for growth lines.

Type material.—Holotype: McLearn, 1932, pl. 5, figs. 1–3. Refigured herein, Pl. 26, fig. 9.

Material.—Twenty-one specimens preserved in sandstone of the upper Fannin Formation.

Measurements.—See Table 44.

Discussion.—This species is placed in *Lioceratoides (Lioceratoides)* because of its ontogenetic sequence of ornamentation change and its fairly involute, compressed shell. The ornamentation is more pronounced and the shell less involute than in *L. (L.) involutum.* In *L. (L.) maurelli,* the shell is less compressed and the ribbing more persistent. *L. (L.)* cf. *grecoi* has a less compressed whorl section, the ribs are coarser, and the division into primaries and secondaries occurs at larger shell diameters.

Occurrence.—*L. (L.) allifordense* has only been recorded from the Queen Charlotte Islands.

Localities.—DT2, D24, D26, E62, E65–68, I03.

Age.—Carlottense Zone (Late Pliensbachian) to early Toarcian.

Lioceratoides (Lioceratoides) cf. **grecoi**
(Fucini, 1901a)
Plate 27, figures 1, 2

cf. *Leioceras? Grecoi* Fucini, 1901a, p. 91, pl. 11, figs. 4, 5.
cf. *Praeleioceras grecoi* Fucini. Fucini, 1931, p. 104, pl. 21, fig. 12.
(?)*Lioceratoides grecoi* (Fucini). Cantaluppi and Savi, 1968, p. 253, pl. 22, figs. 7, 8.
cf. *Lioceratoides grecoi* (Fucini). Wiedenmayer, 1980, p. 90, pl. 14, fig. 1.

Description.—Midvolute forms with an oval whorl section. The umbilical wall is low and steep, the flanks are gently rounded and the arched venter bears a pronounced, simple keel. Ribbing is irregular in strength and consists of simple flexuous ribs mixed with stout primaries that divide into two secondaries low on the flank. The primaries are prosiradiate and the secondaries rursiradiate.

Type material.—Holotype: *Leioceras? grecoi* Fucini, 1901a, pl. 11, fig. 4.

Material.—Two specimens preserved in sandstone of the upper Fannin Formation.

Discussion.—These specimens show the volution and ribbing style of *L. (L.) grecoi* but they are too small to

Table 45.—Measurements of *Lioceratoides* (*Lioceratoides*) *involutum*, new species. All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*
GSC 98644	c58	39.5	6.8	17.2	10.1	25.6	20.0	50.6	50.5
GSC 98716	45.8	45.8	9.2	20.1	11.5	25.1	21.6	47.2	53.2
GSC 98705	22.2	22.2	4.1	18.5	—	—	11.4	51.4	—
	—	—	3.2	—	4.8	—	8	—	60.0

be identified with confidence. At shell diameters greater than the Queen Charlotte Islands material, *L. (L.) grecoi* characteristically undergoes a loss of ornamentation and a modest compression of the whorl section.

Occurrence.—*L. (L.) grecoi* is a Tethyan species recorded from the Spinatum Zone of Italy (Wiedenmayer, 1980).

Localities.—ET5, E62.

Age.—Carlottense Zone (Late Pliensbachian).

Lioceratoides (Lioceratoides) involutum, new species

Plate 26, figures 2–4; Text-figure 39p

Description.—An involute compressed form with a steep umbilical wall that rounds abruptly into the weakly convergent, flat flanks. The venter bears a prominent, simple keel. Ornamentation is subdued and, to an umbilical diameter of approximately 8 mm, consists of forwardly inclined primaries and numerous secondaries that arise almost halfway up the flank, arch across the upper flank, and project weakly onto the venter. At larger diameters only fine growth lines are evident. A smooth aptychus valve is present in the incomplete body chamber of the holotype (Pl. 26, fig. 4c).

Type material.—Holotype: GSC 98716 (Pl. 26, fig. 4). Paratypes: GSC 98644 (Pl. 26, fig. 2), GSC 98705 (Pl. 26, fig. 3). Preserved in calcareous sandstone of the upper Fannin Formation. There are no other specimens.

Measurements.—See Table 45.

Derivation of name.—In reference to the involute shell.

Discussion.—This new species differs from all other species of *Lioceratoides (Lioceratoides)* by its involute shell and fine ornamentation. The most similar species is *Lioceratoides (L.) naumachensis* (Fucini, 1929) from the uppermost Pliensbachian (Emaciatum Zone) of Spain and elsewhere in southern Europe (Braga, 1983). The European species differs by being less involute, more compressed and with ribbing persisting to larger shell diameters.

Table 46.—Measurements of *Lioceratoides* (*Lioceratoides*) *maurelli* (McLearn, 1930). All measurements are in mm.

specimen no.	*DMAX*	*UD*	*WW*	*WH*	*WWWH*
GSC 9052	c72	19.2	c19	33	c57.6

Occurrence.—This species has only been collected from the Upper Pliensbachian of the Queen Charlotte Islands.

Localities.—ET5, E62.

Age.—Carlottense Zone (Late Pliensbachian).

Lioceratoides (Lioceratoides) maurelli

(McLearn, 1930)

Plate 26, figure 1

Harpoceras maurelli McLearn, 1930, p. 4, pl. 1; 1932, p. 63, pl. 7, figs. 4–6.

Description.—A midvolute species with a compressed whorl section bearing a pronounced keel. On the innermost whorls there are broadly spaced primary ribs dividing into two secondary ribs. On later whorls the ribs are sinuous and strongly projected onto the venter. Ribbing becomes more flat-topped and weaker with growth.

Type material.—A single incomplete, septate specimen, the holotype (GSC 9502), preserved in sandstone of the upper Fannin Formation.

Measurements.—See Table 46.

Discussion.—This species was established by McLearn (1930, 1932) based on a single specimen and unfortunately no more specimens have been collected since. We place the species in *Lioceratoides* because of the style and ontogenetic changes seen in the ribbing, although the coiling is a little more evolute and the whorl section somewhat less compressed than is normally the case for this genus.

Occurrence.—This specimen was collected by McLearn from a stratigraphic interval that spans the Pliensbachian-Toarcian boundary as discussed in the biostratigraphy section (Text-fig. 10); its precise age is uncertain.

Locality.—DT2.

Age.—Carlottense Zone (Late Pliensbachian) or Early Toarcian.

Lioceratoides (Lioceratoides) sp. juv.

Plate 26, figures 7, 8; Text-figure 39r

Harpoceras sp. A. McLearn, 1932, p. 66, pl. 7, figs. 1, 2.

Table 47.—Measurements of *Lioceratoides* (*Lioceratoides*) sp. juv. All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*	*PRHW*
GSC 98642	27.5	22.7	6	26.4	5.5	24.2	9.5	41.9	57.9	20
GSC 6489	29.6	25	6.8	27.2	6.0	24.0	c10.3	41.2	58.3	c20

Description.—Midvolute, rapidly expanding form with an ogival whorl section. The umbilical wall is low and very steep; the flanks are flat; and the arched venter bears a prominent, simple keel. The nucleus has blunt, widely spaced primaries bearing two rursiradiate secondaries. At umbilical diameters of 5 mm or so, the ribbing becomes simple, densely spaced, falcoid and flat-topped.

Material.—Four small specimens in sandstone of the upper Fannin Formation.

Measurements.—See Table 47.

Discussion.—This form was first figured by McLearn (1932) based on a single specimen collected in Whiteaves Bay (section D) that McLearn interpreted as an immature *Harpoceras*; the specimen is refigured here (Plate 26, figure 7). The presence of primary and secondary ribs at an early ontogenetic stage together with its now proven geological age (preceding *Harpoceras*) suggest that *Lioceratoides* is a more appropriate generic assignment. Because of its small size, it cannot be confidently identified to the species level; it does not appear to be similar to the nuclei of any of the other species of *Lioceratoides (L.)* described in this report.

Occurrence.—Similar but not identical ammonites have been collected from the Upper Pliensbachian of Oregon and California and figured as *Harpoceras?* sp. by Imlay (1968).

Localities.—DT2, D26, ET5, E67.

Age.—Carlottense Zone (Late Pliensbachian) to early Toarcian.

Subgenus **PACIFICERAS** Repin, 1970

Type species.—*Schloenbachia propinqua* Whiteaves, 1884, p. 274, pl. 33, fig. 2, by original designation (Repin, 1970, p. 42).

Remarks.—Repin (1970) originally established *Pacificeras* as a subgenus of *Ovaticeras* to accommodate Toarcian forms from Russia that have been placed in *Tiltoniceras antiquum* (Wright, 1882) by Howarth (1992). *Schloenbachia propinqua* Whiteaves, 1884, from the Queen Charlotte Islands (on which *Pacificeras* is based) has been reevaluated here because it appears to have a bearing on the evolutionary relationships between the genera *Lioceratoides, Tiltoniceras,* and *Protogrammoceras. Pacificeras, Lioceratoides* and *Tiltoniceras* accommodate forms that are all characterized by a strong simple keel but otherwise represent a morphological spectrum with *Pacificeras* occupying the middle ground.

Lioceratoides consists of midvolute to involute, rapidly expanding forms with compressed whorls. The ornamentation passes through as many as three stages during ontogeny: (1) irregular primary ribs with bifurcating or bundled secondaries on the inner whorls; (2) simple, falcoid, projected and often flattened ribs on intermediate or outer whorls; (3) on some forms the falcoid stage is brief or absent and the shell becomes smooth.

Forms accommodated in *Pacificeras* are less involute and less compressed than forms assigned to *Lioceratoides.* The inner whorls have ribs divided into short primaries and weaker secondaries. At smaller shell diameters than in *Lioceratoides* the ornamentation simplifies into weak, single ribs and the shell rapidly becomes smooth.

Like *Pacificeras, Tiltoniceras* is less involute and less compressed than *Lioceratoides* but ribs are never divided into primaries and secondaries. Simple, flexuous, projected ribs characterize the inner whorls whereas outer whorls are smooth or striate.

Age and distribution.—In North America, *Pacificeras, Lioceratoides,* and *Tiltoniceras* have similar stratigraphic distributions. In the lower part of their ranges, they co-occur with species of *Fanninoceras* and *Amaltheus* (Smith *et al.*, 1988; Thomson and Smith, 1992) indicating a late Pliensbachian age and representing the earliest records for *Tiltoniceras* and *Pacificeras.* In the upper part of their ranges above *Fanninoceras* and *Amaltheus,* they co-occur with species of *Dactylioceras* indicating an early Toarcian age (Smith *et al.*, 1988; Tipper *et al.*, 1991; Jakobs *et al.*, 1994b). Elsewhere, *Lioceratoides* occurs throughout the Tethyan Realm where it is most characteristic of the late Pliensbachian although the last representatives occur in the basal Toarcian (Guex, 1973; Wiedenmayer, 1980). In contrast, *Tiltoniceras* is restricted to higher latitudes where it appears cryptically in the basal Toarcian of Russia and northwest Europe (Howarth, 1992). We suggest that *Tiltoniceras* evolved in the northeast Pacific during the late Pliensbachian, not directly from *Protogrammoceras,* but indirectly via *Lioceratoides* and *Pacificeras.*

Table 48.—Measurements of *Lioceratoides* (*Pacificeras*) *angionus* (Fucini, 1931). All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*
GSC 98611	c53	47	11.5	24.5	—	—	20.5	43.6	—
GSC 99045	c98	76.2	26.7	35.0	19.4	25.5	27.2	35.7	71.3
	—	—	12	—	11.3	—	19	—	59.5
GSC 98634	c56	45	12.5	27.8	11.8	26.2	c19	42.2	62.1
GSC 98640	47	43	12.0	27.9	10.3	24.0	17.0	39.5	60.1
GSC 98732	82	65.2	16.5	25.3	15.8	24.2	27.9	42.8	56.6
MEAN	—	—	—	28.1	—	25.0	—	40.8	61.9
ST. DEV.	—	—	—	4.1	—	1.1	—	3.2	5.6

Lioceratoides (Pacificeras) angionus
(Fucini, 1931)
Plate 27, figures 3–7; Text-figure 39k,o

Praelioceras angionum Fucini, 1931, p. 107, pl. 12, figs. 1–5.
Lioceratoides angionus (Fucini). Guex, 1973, p. 507, pl. 1, fig. 5.

Description.—A midvolute to evolute form characterized by its compressed whorl section that becomes subquadrate with growth. The umbilical wall is steep and rounds abruptly into the flat flanks which are weakly convergent towards the venter until umbilical diameters of approximately 10 mm after which they are almost parallel.

The broad, flat venter bears a prominent, stout keel. Ornamentation is weak consisting of prorsiradiate primaries that divide irregularly into two or three weaker secondary ribs that arch across the upper flank but fade near the ventro-lateral shoulder. On the smaller figured specimens the ribbing has faded to simple growth lines but on the two larger specimens (Pl. 27, figures 4 and 7) ribbing persists to larger shell diameters. Specimen 98732 (Pl. 27, figure 7) is completely septate but specimen 99045 (Pl. 27, figure 4) has part of a body chamber that is beginning to egress.

Type material.—Lectotype: Fucini, 1931, pl. 12, fig. 1.

Material.—Nine specimens in calcareous sandstone of the upper Fannin Formation.

Measurements.—See Table 48.

Discussion.—This species differs from *L. (P.) propinquum* in its whorl shape, notably the steep umbilical wall, parallel flanks and tabulate venter.

There are no firm criteria amongst the collection for judging maturity but it is postulated that the larger figured specimens represent incomplete macroconchs. This question can only be resolved when appropriately well preserved material is collected.

The specimens of *L. (P.) angionus* that have been illustrated in the literature (see synonymy) are all small (up to 40 mm or so shell diameter) so that comparisons with the Queen Charlotte Islands fauna are difficult. The smaller Canadian specimens (Pl. 27, figures 3, 5, 6), with their irregular ribbing quickly declining to growth lines and their steep umbilical wall, compare reasonably well, however.

Occurrence.—*L. (P.) angionus* is known from the Upper Pliensbachian of Italy (Fucini, 1931) and the lowest Toarcian of Morocco (Guex, 1973).

Localities.—D24, ET5, E65, E67, E68.

Age.—Carlottense Zone (Late Pliensbachian).

Lioceratoides (Pacificeras) propinquum
(Whiteaves, 1884)
Plate 28, figures 1–11; Plate 29, figure 1;
Text-figures 38d-g, 39n,q

Schloenbachia propinqua Whiteaves, 1884, p. 247; 1900, pl. 33, figs. 2 and 2a.
Harpoceras propinquum (Whiteaves). McLearn, 1930, p. 4; 1932, p. 66, pl. 6, figs. 1–4; pl. 7, fig. 3; Shimer and Schrock, 1944, pl. 240, figs. 13, 14; Frebold, 1964b, pl. 8, figs. 4, 6, 7.
(?) *Harpoceras* sp. juvenile. Frebold, 1964a, p. 16, pl. 6, figs. 6, 7 only.
non *Ovaticeras propinquum* (Whiteaves). Repin, 1968, p. 116, pl. 44, fig. 1; pl. 45, fig. 1.
non *Tiltoniceras propinquum* (Whiteaves). Dagis, 1971, p. 75, pl. 4, figs. 4, 5; 1974, p. 21, pl. 1, figs. 1–4; pl. 2, fig. 1.
Tiltoniceras propinquum (Whiteaves). Smith, Tipper, Taylor, and Guex, 1988, pl. 5, figs. 1–4; Thomson and Smith, 1992, p. 39, pl. 15, figs. 5–7 only.
Lioceratoides n. sp. Smith, Tipper, Taylor, and Guex, 1988, pl. 5, figs. 7, 8.

Description.—Large, evolute and fairly slowly expanding with a compressed whorl section. The umbilical wall rounds gently into the convex flanks and the arched venter bears a prominent, simple keel. There is considerable variation in the strength of the ribbing within the sample. The early whorls show widely spaced primary ribs developed by fasciculation or bifurcation of secondaries fairly low on the flank. A few intercalated ribs are also present. By umbilical diameters of 7 mm the ribs have become simple, densely spaced and flexuous. They quickly fade, leaving most of the shell smooth except for growth lines.

Type material.—Lectotype: GSC 4877 (Whiteaves, 1900, pl. 33, figs. 2, 2a (refigured herein, Pl. 28, fig. 2).

Table 49.—Measurements of *Lioceratoides* (*Pacificeras*) *propinquum* (Whiteaves, 1884). All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*
GSC 4877	47.6	47.6	16.5	34.7	10.5	22.1	19.2	40.3	54.7
GSC 6490	182	137	62.7	36.2	c33.4	19.3	66.2	38.3	c50.5
		155	57.5	37.1	33.7	21.7	59.7	38.5	56.5
GSC 6491	37.5	32.7	10.0	30.6	8.2	25.1	13.6	41.6	60.3
GSC 87804	63.6	59.0	23.0	39.0	14.6	24.7	23.5	39.8	62.1
GSC 87806	32.2	32.2	9.2	28.6	7.4	23.0	13.5	41.9	54.8
GSC 98655	38.3	30.5	9.2	30.2	7.6	24.9	13.1	43.0	57.6
GSC 98661	38.0	35.6	9.7	27.2	—	—	15.5	43.5	
GSC 98676	20.0	20.0	5.4	27.0	5.5	27.5	9.1	45.5	60.4
GSC 98681	26.9	26.9	7.8	29.0	6.1	22.7	11.3	42.0	54.0
GSC 98682	c28.0	23.0	7.0	30.4	—	—	10.0	43.5	—
GSC 98685	31.3	25.5	8.9	34.9	6.2	24.3	10.2	40.0	60.8
GSC 98687	64.2	56.2	19.4	25.4	13.3	23.7	20.2	35.9	65.8
MEAN	—	—	—	31.6	—	23.5	—	41.1	58.0
ST. DEV.	—	—	—	4.3	—	2.2	—	2.6	4.4

When McLearn designated the lectotype (1932, p. 67) he also recognized two plesiotypes (McLearn, 1932, pl. 6, figs. 1 and 2 and pl. 7, fig. 3). The plesiotypes are refigured herein (GSC 6491, Pl. 28, fig. 7; GSC 6490, Pl. 29, fig. 1).

Material.—143 specimens in sandstone and siltstone of the Fannin Formation.

Measurements.—See Table 49.

Discussion.—When Whiteaves first described this species he indicated that the best preserved figured specimen, which later became the lectotype (McLearn, 1932), originated from South Bay which is now known as Whiteaves Bay (section D herein. p. 14). Unfortunately, the publication of the plate was unexpectedly delayed until part 4 of Whiteaves' work on fossils from the Queen Charlotte Islands (Whiteaves, 1900) in which the fossil was reported to have come from Maude Island (section E herein, p. 15) and this has led to confusion in subsequent literature. From the context of Whiteaves' original description and in agreement with McLearn's conclusion (McLearn, 1932, p. 69), we believe that the specimen did, in fact, originate from Whiteaves Bay.

This large species had been previously reported from North America and Russia but Howarth (1992) has re-evaluated these reports and concludes that the Russian material, with its simpler ribbing, was better accommodated in the species *Tiltoniceras antiquum* (described below). The North American specimens are distinguished by early whorls that have complex ribs followed by simple ribs and then smooth shells, a pattern more akin to *Lioceratoides*. As discussed above, *Pacificeras* with its more evolute and slowly expanding shell, is retained as a subgenus of *Lioceratoides* based on *Schloenbachia propinqua* of Whiteaves (1884) as type (Repin, 1970).

Occurrence.—As interpreted here, *L. (P.) propinquum* is only known from the northeast Pacific.

Localities.—DT2, D24–27, ET5, E62–68, IO3, I12.

Age.—Carlottense Zone (Late Pliensbachian) to early Toarcian.

Genus **TILTONICERAS** Buckman, 1913

Type species.—*Tiltoniceras costatum* Buckman, 1913, p. 8, by original designation. *T. costatum* is a subjective junior synonym of *Harpoceras antiquum* Wright, 1882 (Howarth, 1973, 1992).

Remarks.—See the remarks under *Pacificeras.* The genus has been recently discussed in detail by Howarth (1992) who considers it monospecific.

Age and distribution.—*T. antiquum* first occurs in the upper Pliensbachian of western North America becoming widespread in Boreal, lower Toarcian rocks of northeast Siberia, Germany, and Great Britain.

Tiltoniceras antiquum (Wright, 1882)
Plate 30, figures 1–4; Text-figure 39l-m

Harpoceras antiquum Wright, 1882, pl. 57, figs. 1, 2.

Harpoceras acutum (Tate). Wright, 1884, p. 469, pl. 82, figs. 7, 8.

Ammonites capillatus Denckmann, 1887, p. 60, pl. 1, fig. 7; pl. 4, fig. 3.

Harpoceras schroederi Denckmann, 1893, p. 101.

Tiltoniceras costatum Buckman, 1913, p. viii; 1914, pl. 97, figs. 1–4; Hoffmann, 1968, p. 15, pl. 4, fig. 3; Dagis, 1974, p. 23, pl. 3, figs. 1–4.

Tiltoniceras acutum Tate. Donovan, 1954, p. 51; Hoffman, 1968, p. 13, pl. 3, fig. 4; Lehmann, 1968, p. 56, pl. 19, fig. 6.

Harpoceras sp. juv. Frebold, 1964a, p. 16, pl. 6, figs. 8, 9 only.

Tiltoniceras schroederi (Denckmann). Hoffmann and Martin, 1960, p. 116, pl. 9, figs. 6, 7, 12; Hoffmann, 1968, p. 13, pl. 4, fig. 2.

Ovaticeras facetum Repin, 1966, p. 45, pl. 1, figs. 4, 5, 8; 1968, p. 115, pl. 46, figs. 1, 2, 4, 5.

Tiltoniceras capillatum (Denckmann). Hoffmann, 1968, p. 17, pl. 5, figs. 1–4; Lehmann, 1968, p. 57, pl. 20, figs. 1, 2, 8; Dagis, 1974, p. 25, pl. 3, figs. 5, 6.

Table 50.—Measurements of *Tiltoniceras antiquum* (Wright, 1882). All measurements are in mm.

specimen no.	*DMAX*	*D*	*UD*	*U*	*WW*	*WWD*	*WH*	*WHD*	*WWWH*
GSC 98713	39.0	32.0	7.9	24.7	7.8	24.4	15.6	48.8	50
GSC 98728	c158	150.8	41.0	27.2	35.4	23.4	65.7	43.5	53.9
GSC 98730	—	45.7	11.8	25.8	11.1	24.3	21.8	47.7	50.9
GSC 98731	59.5	59.5	17.5	29.4	—	—	23.6	39.7	—
		48.0	12.0	25.0	11.7	24.4	20.5	42.7	42.7
MEAN	—	—	—	26.4	—	24.1	—	44.5	49.4
ST. DEV.	—	—	—	1.9	—	0.5	—	3.7	4.8

Ovaticeras propinquum (Whiteaves). Repin, 1968, p. 116, pl. 44, fig. 1; pl. 45, fig. 1.

Tiltoniceras propinquum (Whiteaves). Dagis, 1971, p. 175, pl. 4, figs. 4, 5; 1974, p. 21, pl. 1, figs. 1–4; pl. 2, fig. 1; Thomson and Smith, 1992, p. 39, pl. 15, figs. 4, 8 and 9 only.

Tiltoniceras antiquum (Wright). Schlegelmilch, 1976, p. 88, pl. 46, figs. 5, 6; Howarth, 1992, p. 70, Text-figures 13, 18; pl. 5, fig. 3; pl. 6, figs. 1–8; pl. 7, figs. 1–3, 9.

(?)*Ovaticeras* sp. cf. *O. ovatum* (Young and Bird). Poulton, 1991, p. 20, pl. 13, figs. 7, 11.

(?)*Harpoceras?* sp. Poulton, 1991, p. 20, pl. 13, fig. 8 only.

Description.—Midvolute, large and thick-shelled form with compressed whorls bearing a prominent, simple keel. The umbilical wall is gently sloped, the umbilical shoulder indistinct and the flanks gently convex.

Ribs are fine and simple. They are prorsiradiate and sinuous across the flank and projected ventrally. Ribbing fades at umbilical diameters of 8 mm or so to be replaced by a smooth or striate shell.

Type material.—Lectotype: Wright, 1882, pl. 57, figs. 1 and 2 designated by Donovan (1954, p. 44) and refigured by Howarth (1992, Text-fig. 13).

Material.—Seventy-five specimens from the upper Fannin Formation.

Measurements.—See Table 50.

Discussion.—This species reaches a large size as exemplifed by the specimen figured on Plate 30, figure 1 which has a diameter of almost 160 mm and yet is still septate. Three other similarly large and completely septate specimens also occur in the collection but most are incomplete and less than 50 mm in shell diameter. An exception, indicating the presence of dimorphism, is figured on Plate 30, figure 4. This specimen has a diameter of almost 60 mm and a body chamber just under half a whorl in length. The body chamber, which egresses slightly, has a peristome that is sinuous, in harmony with the now obsolete ribbing; it flares in the central part of the flank end projects ventrally to form a rostrum. One other, unfigured specimen reaches a diameter of over 78 mm and has a body chamber length of about half a whorl. The peristome is mostly incomplete but where it remains it shows a similar flaring.

T. antiquum differs from *Lioceratoides (Pacificeras) propinquum* in being slightly more involute and more rapidly expanding and in having ribs that are never divided into primaries and secondaries. *L. (P.) angionus* also has more complex ribbing on its earlier whorl and is further characterized by its steep umbilical wall and more pronounced umbilical shoulder.

Occurrence.—As discussed in the introduction to *Pacificeras* (p. 70), *T. antiquum* is characteristic of the Boreal Realm where it normally occurs in the basal Toarcian. In the Queen Charlotte Islands and elsewhere in Canada it also occurs in the uppermost Pliensbachian and presumably it had its origin within *Lioceratoides.*

Localities.—B06, DT2, D27, ET5, E62–68.

Age.—Carlottense Zone (Late Pliensbachian) and early Toarcian.

APPENDIX

LOCALITY REGISTER

A brief geographical description, latitude, longitude, and 1:50,000 map sheet are given for stratigraphic sections and locality numbers cited in the text; type numbers are also listed by locality. Refer to Text-figures 2 and 3 for locations.

SECTION A: KUNGA ISLAND (Text-figures 2, 7 and 16)

Localities A01 to A13 in a stratigraphic sequence exposed along the southeast shore of Kunga Island, 52°45′53″N, 131°33′08″W; NTS 103B/13 & 14, Louise Island.

A01	UBC loc. PLS-14, Sandilands Formation
A02	UBC loc. PLS-13, Ghost Creek Formation
A03	UBC loc. PLS-12, Ghost Creek Formation
A04	UBC loc. PLS-11, Ghost Creek Formation
A05	UBC loc. PLS-10, Ghost Creek Formation
A06	UBC loc. PLS-9, Ghost Creek Formation
A07	UBC loc. PLS-8, Ghost Creek Formation
A08	UBC loc. PLS-7, Ghost Creek Formation
A09	UBC loc. PLS-6, Rennell Junction Member (of the Fannin Formation)
A10	UBC loc. PLS-5, Rennell Junction Member
A11	UBC loc. PLS-4, Rennell Junction Member

A12 UBC loc. PLS-2, Rennell Junction Member
A13 UBC loc. PLS-1, Rennell Junction Member

SECTION B: LOUISE ISLAND (Text-figures 2, 8 and 17)

Localities BT1 (talus), and B01 to B06 in a stratigraphic sequence exposed on the north shore of Louise Island at Renner Point, between 53°02′03″N, 131°52′48″W and 53°02′06″N, 131°52′47″W; NTS 103G/4, Cumshewa.

BT1 GSC loc. C-117025, GSC type 98702, Ghost Creek Formation
B01 GSC loc. C-117022, Ghost Creek Formation
B02 GSC loc. C-117021, Ghost Creek Formation
B03 GSC loc. C-117020, Rennell Junction Member
B04 GSC loc. C-117019, GSC types 95575, 98626, 98627, 98628, 98629, 98630, 98633, 98636, 98637, 98639, Rennell Junction Member
B05 GSC loc. C-117018, Fannin Formation
B06 GSC loc. C-117017, Fannin Formation

SECTION C: CUMSHEWA INLET (Text-figures 2, 9 and 18)

Localities CT1, CT2 (talus), and C01 to C05 in a stratigraphic sequence exposed on the north shore of Cumshewa Inlet, 53°02′53″N, 131°56′05″W; NTS 103G/4, Cumshewa.

CT1 GSC loc. C-157644, Ghost Creek Formation
GSC loc. C-157645, Ghost Creek Formation
CT2 GSC loc. C-157607, Ghost Creek Formation
GSC loc. C-157647, Ghost Creek Formation
GSC loc. C-157648, Ghost Creek Formation
C01 GSC loc. C-157609, Ghost Creek Formation
GSC loc. C-157650, Ghost Creek Formation
C02 GSC loc. C-117026, Rennell Junction Member
GSC loc. C-157671, Rennell Junction Member
C03 GSC loc. C-80610, GSC type 87797, Fannin Formation
GSC loc. C-117027, GSC type 98692, Fannin Formation
GSC loc. C-157668, Fannin Formation
GSC loc. C-157670, Fannin Formation
C04 GSC loc. C-157612, Fannin Formation
C05 GSC loc. C-157649, Fannin Formation

SECTION D: WHITEAVES BAY (Text-figures 2, 10 and 19)

Localities DT1, DT2 (talus), and D01 to D28 in a stratigraphic sequence exposed in Whiteaves Bay on the north shore of Moresby Island, 53°11′N, 132°01′W; NTS 103F/1, Skidegate Inlet.

DT1 GSC loc. O-48564, GSC types 87800, 98673, 98674, 98675, 99020, Fannin Formation
DT2 GSC loc. O-13630, GSC type 9052, 99046, Fannin Formation
GSC loc. C-117033, GSC types 4877, 6489, 6490, 6491, 9053, Fannin Formation
D01 GSC loc. O-93568, Ghost Creek Formation
D02 GSC loc. C-80242, Ghost Creek Formation
D03 GSC loc. O-93565, GSC types 98688, 98691, Ghost Creek Formation
GSC loc. C-80243, Ghost Creek Formation
D04 GSC loc. C-80244, Ghost Creek Formation
D05 GSC loc. C-80245, Ghost Creek Formation
D06 GSC loc. C-80246, GSC type 98656, Ghost Creek Formation
GSC loc. C-80247, Ghost Creek Formation
D07 GSC loc. C-80248, Ghost Creek Formation
GSC loc. C-80249, GSC types 98695, 98707, Ghost Creek Formation
GSC loc. C-80250, Ghost Creek Formation
GSC loc. C-80751, Ghost Creek Formation
GSC loc. C-80752, Ghost Creek Formation
D08 GSC loc. O-93564, GSC types 98654, 98693, 99044, Ghost Creek Formation
GSC loc. C-80753, Ghost Creek Formation
D09 GSC loc. O-93571, Ghost Creek Formation
D10 GSC loc. C-80754, Ghost Creek Formation
D11 GSC loc. O-93575, GSC type 95573, Ghost Creek Formation
GSC loc. C-80755, GSC type 98645, Ghost Creek Formation
D12 GSC loc. C-80756, Ghost Creek Formation
D13 GSC loc. C-80757, Ghost Creek Formation
D14 GSC loc. C-80758, Rennell Junction Member
D15 GSC loc. C-80759, Rennell Junction Member
D16 GSC loc. C-80760, Rennell Junction Member
D17 GSC loc. C-80761, Rennell Junction Member
D18 GSC loc. O-93563, Rennell Junction Member
D19 GSC loc. C-80764, Fannin Formation
D20 GSC loc. C-80765, GSC types 99018, 98590, 98619, 98620, 98742, Fannin Formation
D21 GSC locs. C-80766, Fannin Formation
D22 GSC loc. C-80768, GSC type 98584, Fannin Formation
D23 GSC loc. C-80769, Fannin Formation
D24 GSC loc. O-93574, GSC types 98643, 98732, 98733, 98739, Fannin Formation
GSC loc. C-80771, Fannin Formation
D25 GSC loc. C-80772, GSC type 98740, Fannin Formation
D26 GSC loc. O-93582, GSC type 98642, Fannin Formation
GSC loc. C-80773, Fannin Formation
D27 GSC loc. C-80774, Fannin Formation
GSC loc. C-80776, GSC type 98746, Fannin Formation
D28 GSC loc. C-80775, Fannin Formation

SECTION E: MAUDE ISLAND (Text-figures 2, 11 and 20)

Localities ET1 to ET5 (talus), and E01 to E79 in a stratigraphic sequence exposed in Fannin Bay on the southeast side of Maude Island, 53°12′N, 132°03′W; NTS 103F/1, Skidegate Inlet.

ET1 GSC loc. O-48603, GSC types 20337, 87810, 98631, 98632, 98689
GSC loc. O-93577, GSC type 98667
GSC loc. O-93743, GSC type 98575
GSC loc. O-93748
GSC loc. C-80836, GSC types 87811, 98657, Fannin Formation
ET2 GSC locs. O-52342, O-93744, Rennell Junction Member
ET3 GSC locs. C-80835, C-80837, C-80838, Rennell Junction Member
GSC loc. C-80840, GSC types 98625, 98696, Rennell Junction Member
GSC locs. C-80841, C-80844, C-80845, C-81916, C-118698, Rennell Junction Member
ET4 GSC loc. O-13628, GSC types 98576, 98577, 98579, 98594, Fannin Formation
GSC loc. O-48573, GSC types 87798, 98578, Fannin Formation
GSC loc. O-93579, GSC type 98709, Fannin Formation
GSC loc. O-93741, GSC type 98581, 98622, Fannin Formation
GSC loc. C-80839, GSC types 98597, 98610, Fannin Formation
GSC loc. C-81724, GSC type 98608, Fannin Formation
GSC loc. C-117032, GSC types 6493, 6494, 6495, 6496, 6517, 6518, 9054, 9058, 98684, Fannin Formation
GSC loc. C-117034, GSC types 4876, 4879, 6519, 6670, 9055, Fannin Formation
ET5 GSC loc. O-48563, GSC type 98716, Fannin Formation

GSC loc. O-93578, Fannin Formation
GSC loc. C-80814, GSC type 98598, Fannin Formation
GSC loc. C-80824, GSC type 98685, Fannin Formation
GSC loc. C-80831, GSC type 98586, Fannin Formation
GSC loc. C-80832, GSC type 98694, Fannin Formation
GSC loc. C-80833, GSC type 99040, Fannin Formation
GSC loc. C-80834, GSC types 98585, 98744, Fannin Formation
GSC loc. C-81917, GSC type 98644, Fannin Formation
GSC loc. C-117002, GSC types 98677, 98718, 98730, Fannin Formation. Ammonites found together in a single boulder.
GSC loc. C-117003, GSC types 87804, 87806, 87809, 98676, 98697, 99045, Fannin Formation. Ammonites found together in a single boulder.
GSC loc. C-117004, Fannin Formation. Ammonites found together in a single boulder.
GSC loc. C-117005, 98589, 98731, 99015, Fannin Formation. Ammonites found together in a single boulder.
GSC loc. C-117030, Fannin Formation
GSC loc. C-117031, GSC types 4878, 87807, 98728, 98734, 98735, Fannin Formation
UBC loc. 82–14, Fannin Formation
E01 GSC loc. C-80241, GSC type 98650, Ghost Creek Formation
GSC locs. O-91819, C-80315, Ghost Creek Formation
E02 GSC loc. C-80318, Ghost Creek Formation
E03 GSC loc. C-80319, Ghost Creek Formation
E04 GSC locs. C-80321, C-80323, Ghost Creek Formation
E05 GSC loc. C-80324, Ghost Creek Formation
E06 GSC loc. O-91820, Ghost Creek Formation
E07 GSC locs. O-91821, C-80325, Ghost Creek Formation
E08 GSC locs. O-91822, C-80326, Ghost Creek Formation
E09 GSC loc. O-91823, Ghost Creek Formation
E10 GSC loc. C-80328, Ghost Creek Formation
E11 GSC loc. O-91824, Ghost Creek Formation
E12 GSC loc. O-91825, Ghost Creek Formation
E13 GSC loc. O-91805, Ghost Creek Formation
GSC loc. C-80329, GSC type 98660, Ghost Creek Formation
E14 GSC loc. O-91799, Ghost Creek Formation
GSC loc. C-80330, GSC type 98665, Ghost Creek Formation
E15 GSC loc. O-91796, Ghost Creek Formation
E16 GSC loc. C-80331, Ghost Creek Formation
E17 GSC loc. C-80332, Rennell Junction Member
E18 GSC loc. O-91797, Rennell Junction Member
E19 GSC loc. C-80333, Rennell Junction Member
E20 GSC loc. O-91803, GSC type 98664, Rennell Junction Member
E21 GSC loc. C-80334, Rennell Junction Member
E22 GSC loc. O-91802, Rennell Junction Member
E23 GSC locs. O-91801, C-80336, Rennell Junction Member
E24 GSC loc. O-91798, Rennell Junction Member
E25 GSC locs. O-91793, C-80337, Rennell Junction Member
E26 GSC loc. O-91795, Rennell Junction Member
E27 GSC loc. O-91794, GSC types 87790, 87791, 95576, 98653, Rennell Junction Member
GSC loc. C-80338, Rennell Junction Member
E28 GSC loc. C-80340, Rennell Junction Member
E29 GSC loc. C-80341, Rennell Junction Member
E30 GSC locs. C-80342, C-80343, C-90555, Rennell Junction Member
E31 GSC loc. C-80344, Rennell Junction Member
E32 GSC loc. O-91807, GSC type 78715, Rennell Junction Member
E33 GSC loc. O-91811, Rennell Junction Member
E34 GSC locs. O-91815, C-80345, Rennell Junction Member
GSC loc. O-91814, GSC type 98648, Rennell Junction Member
E35 GSC loc. O-91810, Rennell Junction Member
E36 GSC loc. C-80346, Rennell Junction Member
E37 GSC loc. C-80347, Rennell Junction Member
E38 GSC loc. C-80348, GSC type 98703, Rennell Junction Member
E39 GSC loc. C-80349, Rennell Junction Member
E40 GSC loc. C-80350, GSC type 98669, Rennell Junction Member
E41 GSC loc. C-80215, Rennell Junction Member
E42 GSC loc. C-80216, Rennell Junction Member
E43 GSC loc. C-80217, Rennell Junction Member
E44 GSC loc. O-91818, Rennell Junction Member
E45 GSC locs. C-80219, C-80220, Rennell Junction Member
E46 GSC loc. C-80221, Rennell Junction Member
E47 GSC loc. C-80222, Rennell Junction Member
E48 GSC loc. C-90554, GSC type 98686, Rennell Junction Member
E49 GSC loc. C-80223, Rennell Junction Member
E50 GSC loc. C-80224, Fannin Formation
E51 GSC loc. C-80226, Fannin Formation
GSC loc. C-117284, GSC type 98670, Fannin Formation
E52 GSC loc. C-90553, GSC types 87801, 98583, Fannin Formation
E53 GSC loc. C-80228, GSC type 98701, Fannin Formation
E54 GSC loc. C-80229, Fannin Formation
E55 GSC loc. O-91827, GSC types 98574, 98607, Fannin Formation
GSC locs. C-80231, C-80232, Fannin Formation
E56 GSC loc. O-91828, Fannin Formation
GSC loc. C-80233, GSC type 98623, Fannin Formation
E57 GSC loc. C-80234, GSC types 98614, 98615, 98616, 98617, 98624, Fannin Formation
GSC loc. C-90614, GSC types 87796, 98672, 98706, 98708, Fannin Formation
E58 GSC loc. C-80235, Fannin Formation
E59 GSC loc. O-91830, Fannin Formation
E60 GSC loc. C-80240, Fannin Formation
E61 GSC loc. C-80825, GSC type 98698, Fannin Formation
E62 GSC loc. O-91792, Fannin Formation
GSC loc. C-81716, GSC types 87805, 98679, 98687, 98705, 98729, 99016, Fannin Formation
E63 GSC loc. O-91816, Fannin Formation
GSC loc. O-93750, GSC types 98588, 98600, 98727, 98745, Fannin Formation
GSC loc. C-90545, GSC types 98613, 98649, 98681, 98682, 98741, 99017, Fannin Formation
E64 GSC loc. O-91832, GSC type 99046, Fannin Formation
GSC loc. O-91833, Fannin Formation
E65 GSC loc. O-91834, Fannin Formation
GSC loc. O-91835, GSC types 98640, 98736, Fannin Formation
GSC loc. C-80783, GSC type 98611, Fannin Formation
GSC loc. C-90544, GSC type 98713, Fannin Formation
E66 GSC locs. C-80784, C-80818, Fannin Formation
GSC loc. C-80817, GSC type 98690, Fannin Formation
E67 GSC loc. C-80785, GSC types 98634, 98641, 98655, 98661, Fannin Formation
GSC loc. C-80815, Fannin Formation
E68 GSC loc. C-80786, GSC type 87808, Fannin Formation
GSC loc. C-90615, Fannin Formation

SECTION F: ROAD 19 QUARRY (Text-figures 3, 12 and 21)

Localities FT1 and FT2 (talus), and F01 to F12 in a stratigraphic sequence measured in a quarry on the north side of Forest Road 19 at 53°22′30″, 132°16′00″; NTS 103F/8, Yakoun River.

FT1 GSC loc. C-156675, GSC types 98710, 98738, 99027, 99038, 99041, 99042, 99043, Rennell Junction Member

GSC loc. C-177370, GSC types 87809, 98651, 98671, 99022, 99023, 99024, 99039, Rennell Junction Member

FT2 GSC loc. C-56954, GSC types 98711, 99013, 99014, Fannin Formation
GSC loc. C-177368, types 98592, 99032, 99033, 99034, 99035, 99036, 99037, Fannin Formation

F01 GSC loc. C-177371, Rennell Junction Member
F02 GSC loc. C-177369, Rennell Junction Member
F03 GSC loc. C-177358, Rennell Junction Member
F04 GSC loc. C-177359, Rennell Junction Member
F05 GSC loc. C-177360, Rennell Junction Member
F06 GSC loc. C-177361, Rennell Junction Member
F07 GSC loc. C-177367, Rennell Junction Member
F08 GSC loc. C-177362, Fannin Formation
F09 GSC loc. C-177363, Fannin Formation
F10 GSC loc. C-177364, Fannin Formation
F11 GSC loc. C-177365, Fannin Formation
F12 GSC loc. C-177366, Fannin Formation

SECTION G: RENNELL JUNCTION (Text-figures 3, 13 and 22)

Localities GT1 to GT4 (talus), and G1 to G11 in a stratigraphic sequence measured in a gulley on the east side of the Graham Island main road near its junction with the Rennell Sound road at 53°24′26″N, 132°18′13″W; NTS 103F/8, Yakoun River.

GT1 GSC loc. C-81923, Ghost Creek Formation
GSC loc. C-90574, Ghost Creek Formation
GSC loc. C-90579, GSC types 98668, 98704, Rennell Junction Member
GSC loc. C-90589, Ghost Creek Formation
GT2 GSC loc. C-90573, Rennell Junction Member
GSC loc. C-90604, Rennell Junction Member
GT3 GSC loc. C-81712, GSC types 87792, 98638, 98671, 99047, Rennell Junction Member
GSC loc. C-90587, GSC type 87794, Rennell Junction Member
GSC loc. C-90588, Ghost Creek Formation
GSC loc. C-118697, GSC type 98635, Rennell Junction Member
GT4 GSC loc. C-81927, GSC types 87799, 98596, 98603, 98717, 98719, Fannin Formation
G01 GSC loc. C-81926, GSC type 98666, Ghost Creek Formation
GSC loc. C-90549, GSC type 98663, Ghost Creek Formation
GSC loc. C-90978, GSC type 98658, Ghost Creek Formation
G02 GSC loc. C-81925, Ghost Creek Formation
GSC loc. C-90548, Ghost Creek Formation
GSC loc. C-90556, GSC type 87788, Ghost Creek Formation
GSC loc. C-90591, Ghost Creek Formation
G03 GSC loc. C-81924, Ghost Creek Formation
GSC loc. C-90547, GSC type 98659, Ghost Creek Formation
G04 GSC loc. C-81922, Ghost Creek Formation
GSC loc. C-90572, Ghost Creek Formation
G05 GSC loc. C-90575, Ghost Creek Formation
GSC loc. C-90580, GSC type 98646, Ghost Creek Formation
G06 GSC loc. C-90581, Rennell Junction Member
G07 GSC loc. C-90551, Rennell Junction Member
G08 GSC loc. C-90583, Rennell Junction Member
G09 GSC loc. C-90590, Rennell Junction Member
G10 GSC locs. C-90593, C-90618, Rennell Junction Member
G11 GSC loc. C-90592, Rennell Junction Member

SECTION H: INTERCOAST RESOURCES BOREHOLE DDH-179 (Text-figures 3, 14 and 23)

Localities H1 to H12 in a sequence recovered from a borehole at 53°24′29″N, 132°18′11″W; NTS 103F/8, Yakoun River.

H01 GSC loc. C-90539, Ghost Creek Formation
H02 GSC loc. C-90535, Ghost Creek Formation
H03 GSC loc. C-90640, Ghost Creek Formation
H04 GSC loc. C-90976, Ghost Creek Formation
H05 GSC loc. C-90642, GSC type 98647, Ghost Creek Formation
H06 GSC loc. C-116300, Ghost Creek Formation
H07 GSC loc. C-90534, Rennell Junction Member
H08 GSC loc. C-90611, Rennell Junction Member
H09 GSC loc. C-90641, Rennell Junction Member
H10 GSC loc. C-90538, Rennell Junction Member
H11 GSC loc. C-90530, Rennell Junction Member
H12 GSC loc. C-90610, Rennell Junction Member

ISOLATED LOCALITIES (Text-figures 3 and 24)

Localities I01 to I17 in southern Graham Island; NTS 103F/8, Yakoun River.

I01 53°23′00″N, 132°15′30″W
GSC loc. C-81741, Rennell Junction Member. Ammonites not associated with each other.
I02 53°22′42″N, 132°16′08″W
GSC loc. O-93721, GSC types 98582, 98683, Rennell Junction Member.
GSC loc. O-93725, Rennell Junction Member.
I03 53°23′13″N, 132°16′16″W
GSC loc. C-90560, Fannin Formation
GSC loc. C-90559, GSC type 98747, Fannin Formation
GSC loc. C-90557, Fannin Formation
I04 53°24′11″N, 132°16′08″W
GSC loc. O-93724, Ghost Creek Formation
I05 53°24′29″N, 132°15′41″W
GSC loc. O-93723, GSC type 98712, Fannin Formation
I06 53°24′42″N, 132°14′54″W
GSC loc. C-81709, Fannin Formation
GSC loc. C-90542, GSC types 98587, 98591, 98601, 98602, 98604, 98605, 98612, 98621, 98714, 98720, 98721, 98723, 98743, 99019, 99021, Fannin Formation
GSC loc. C-90552, Fannin Formation
I07 53°24′13″N, 132°18′14″W. From a short stratigraphic interval spanning the contact between the Rennell Junction Member and the Fannin sandstones. Localities 81718 and 177356 are from the same interval at the top of the former; 177355 near the base of the latter.
GSC loc. C-81718, Rennell Junction Member
GSC loc. C-177355, GSC types 99025, 99026, 99028, 99029, 99030, 99031, Fannin Formation.
GSC loc. C-177356, Rennell Junction Member.
I08 53°24′36″N, 132°17′43″W
GSC loc. C-81733, GSC types 87784, 87785, Ghost Creek Formation
GSC loc. C-90974, GSC types 87789, 98699, Ghost Creek Formation
GSC loc. C-90977, GSC types 87783, 87793, 95574, 98652, 98662, 98680, Ghost Creek Formation
GSC loc. C-157551, GSC types 95572, 98700, 98715, 98737, Ghost Creek Formation
I09 53°24′50″N, 132°18′11″W
GSC loc. C-81707, GSC type 98678, Ghost Creek Formation
GSC loc. C-90979, Ghost Creek Formation
I10 53°24′57″N, 132°17′49″W
GSC loc. C-90980, Ghost Creek Formation
I11 53°25′16″N, 132°17′43″W
GSC loc. O-93732, Ghost Creek Formation
I12 53°25′18″N, 132°18′24″W

GSC loc. C-81739, Fannin Formation

I13 53°25′11″N, 132°18′46″W
GSC loc. O-93729, Ghost Creek Formation

I14 53°25′46″N, 132°17′16″W
GSC loc. C-81730, GSC types 98580, 98595, 98618, 98724, Fannin Formation

I15 53°25′45″N, 132°17′19″W
GSC loc. C-90612, Fannin Formation

I16 53°25′45″N, 132°17′22″W
GSC loc. C-81727, Ghost Creek Formation
GSC loc. C-90616, Rennell Junction Member

I17 53°25′34″N, 132°18′30″W
GSC loc. C-81703, GSC types 95577, 98593, 98599, 98606, 98609, 98722, 98725, 98726, Fannin Formation
GSC loc. C-81734, Fannin Formation

REFERENCES CITED

Arkell, W. J.
1950. A classification of the Jurassic ammonites. Journal of Paleontology, vol. 24, pp. 354–364.

Arthur, A. J.
1985. Biostratigraphy of the Lower to Middle Jurassic sediments, Ashcroft area, south-central British Columbia. unpublished BS thesis, University of British Columbia, 50 pp., 6 pls.

Bengston, P.
1988. Open nomenclature. Palaeontology, vol. 31, pp. 223–227.

Bettoni, A.
1900. Fossili domeriani della provincia di Brescia. Mémoires de la Société Paléontologique Suisse, vol. 27, 88 pp., 9 pls., 6 text-figs.

Blasco, G., Levy, R., and Nullo, F.
1978. Los amonites de la formacion Osta Arena (Liasico) y su posicion estratigráfica—Pampa de Agnia—(Provincia del Chubut). Congreso Geológico Argentino VII, Neuquén, Argentina, Actas, vol. 2, pp. 407–429.

Blau, J., and Meister, C.
1991. Liassic (Pliensbachian) ammonites from the Lienz Dolomites (Eastern Tyrol, Austria). Jahrbuch für Geologie, Reihe B, pp. 171–204.

Bown, P.
1991. Calcareous nannofossils from the Late Triassic-Early Jurassic of the Queen Charlotte Islands, British Columbia. Geological Survey of Canada, Current Research, 91-1E, pp. 13–18.

Braga, J. C.
1983. Ammonites del Domerense de la Zona Subbética (Cordilleras Béticas, sur de España). unpublished PhD thesis, University of Granada, Granada, Spain, 410 pp., 197 text-figs., 16 pls.

Braga, J. C., Jiminéz, A. P., and Rivas, P.
1982. Los Hildoceratidae del tránsito Domerense-Toarciense de la Zona Subbética (Cordilleras Béticas, S. de España). Boletin de la Reale Sociedad Española de Historia Naturale (Geol.), vol. 80, pp. 133–152.

Braga, J. C., Comas-Rengifo, M. J., Goy, A., and Rivas, P.
1982. Comparaciones faunisticas y correlaciones en el Pliensbachiense de la Zona Subbética y Cordillera Ibérica. Boletin de la Reale Sociedad Española de Historia Naturale, Seccion Geologica, vol. 80, pp. 221–224.
1985. Le Pliensbachien dans la chaîne cantabrique orientale entre Castillo Pedroso et Reinosa (Santander, Espagne). Les Cahiers de L'Institut Catholique de Lyon, vol. 14, pp. 69–83, 2 pls.

Braga, J. C., and Rivas, P.
1985. The mediterranean *Tropidoceras* (Ammonitina) in the Betic Cordilleras. Eclogae Geologicae Helvetiae, vol. 78, pp. 567–605.

Bremer, H.
1965. Zur Ammonitenfauna und Stratigraphie des unteren Lias (Sinemurium bis Carixium) in der Umgebung von Ankara. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, vol. 122, pp. 127–221.

Buckman, S. S.
1909–1930. Yorkshire type ammonites, I-II, and type ammonites, III-VII. Reprinted 1976, Wheldon and Wesley Ltd. and Verlag von Cramer, Herts., England. vol. I, pls. 24–44 (1911); vol. II, 16 pp., pls. 68–90 (1913); pls. 130A–130C (1919); vol. III, pls. 148–194 (1920); vol. IV, 67 pp., pls. 267B-362 (1922); pls. 363–422 (1923); vol. V, 88 p., pls. 458–536 (1924).
1918. Jurassic chronology, I-Lias. Quarterly Journal of the Geological Society of London, vol. 73, pp. 257–327, pls. 26–31.

Callomon, J.
1984. Biostratigraphy, chronostratigraphy and all that—again. *in* 2nd International Symposium on Jurassic Stratigraphy. R. B. Rocha and A. F. Soares, *eds.*, vol. 3, pp. 611–624, Lisbon.

Cameron, B. E. B., and Tipper, H. W.
1985. Jurassic stratigraphy of the Queen Charlotte Islands, British Columbia. Geological Survey of Canada, Bulletin 365, 49 pp.

Cantaluppi, G.
1966. Fossili sinemuriani e domeriani nel "corso bianco" ad est di Brescia. Atti dell'Instituto Geologico della Universita di Pavia, vol. 17, pp. 103–120, pls. 1–2.
1970. Le Hildoceratidae del Lias medio delle regioni mediterranee. Memoirie della Società italiana di Scienze naturali e del Museo Civico di Storia naturale di Milano, vol. 19, pp. 7–46.
1972. Revisione di "*Grammoceras bassanii*" controversa specie-tipo dei generi d'ammoniti *Protogrammoceras* e *Bassaniceras*. Atti della Società italiana di Scienze naturali e del Museo Civico di Storia naturale di Milano, vol. 113, pp. 335–356, pls. 15–16.

Cantaluppi, G., and Brambilla, G.
1968. Le ammoniti del Ripiantino (Saltrio) e della Breggia (Canton Ticino); riflessi biostratigrafici sul Domeriano ed il suo limite inferior. Atti della Società italiana di Scienze naturali e del Museo Civico di Storia naturale di Milano, vol. 107, pp. 277–315.

Cantaluppi, G., and Montanari, L.
1971. Quadro biostratigrafico conclusivo del Carixiano e suopassaggio al Domeriano nelle Prealpi lombarde occiden-

tali. Bolletino della Società Paleontologia Italiana, vol. 10, No. 2, pp. 43–74, 12 pls.

Cantaluppi, G., and Savi, A.
1968. Le ammoniti di Molino Grasso d'Olona (Varesotto); riflessi biostratigrafici sul Domeriano ed il suo limite superiore. Atti della Società italiana di Scienze naturali e del Museo Civico di Storia naturale di Milano, vol. 107, pp. 205–261, pls. 18–21.

Carter, E. S., Cameron, B. E. B., and Smith, P. L.
1988. Lower and Middle Jurassic radiolarian biostratigraphy and systematic paleontology, Queen Charlotte Islands, British Columbia. Geological Survey of Canada, Bulletin 386, 108 pp.

Cólera, I., Rivas, P., Sequeiros, L., and Valenzuela, R.
1978. Algunos *Metaderoceras* (Ammonitina) del Lias inferior de Almonacid de la Cuba (provincia de Zaragoza, Cordillera Ibérica). Estudios Geologicos, vol 34, pp. 309–317, pls. 1–2.

Corvalán, J. I.
1962. Early Mesozoic biostratigraphy of the Westgate area, Churchill County, Nevada. unpublished PhD thesis, Stanford University, Stanford, CA, 224 pp.

Cuvier, G.
1797. Tableau élémentaire de l'histoire naturelle des animaux. 710 pp., 14 pls., Paris.

Dacqué, E.
1934. Leitfossilien. *in* G.Gürich, *ed.*, vol. 7, part 2, pp. 273–582, pls. 25–48. Berlin.

Dagis, A. A.
1971. Genetic relationships between the Toarcian ammonoid genera *Tiltoniceras, Eleganticeras* and *Harpoceras.* Palaeontological Journal, vol. 5, pp. 175–180.
1974. Toarcian ammonites (Hildoceratidae) from the north of Siberia. Transactions of the Institute of Geology and Geophysics, Academy of Science, USSR, Siberian branch, vol. 99, 188 pp., 19 pls. (in Russian).
1976. Late Pliensbachian ammonites (Amaltheidae) of north Siberia. Transactions of the Academy of Science, USSR, Siberian branch, Novosibirsk, 59 pp., 8 text-figs., 17 pls. (in Russian).

Dean, W. T., Donovan, D. T., and Howarth, M. K.
1961. The Liassic ammonite zones and subzones of the northwest European province. Bulletin of the British Museum (Natural History), Geology Series, vol. 4, pp. 435–505, pls. 63–74.

Del Campana, D.
1900. I Cefalopodi del Medolo di Valtrompia. Bolletino della Società Geologica Italiana, vol. 19, pp. 555–644.

Denckmann, A.
1887. Uber geognostischen Verhaltnisse der Umgegend van Dörnten nordlich Goslar, mit besonderer Berücksichtigung der Fauna des oberen Lias. Abhandlungen der geologischen Specialkarte von Preussen und der Thuringischen Staaten, Berlin, vol. 8, 108 pp., 10 pls.
1893. Studien im Deutschen Lias. Jahrbuch der kaiserlichen Preussischen Geologischen Landesanstalt und Bergakademie zu Berlin, vol. 13, pp. 98–114.

Dommergues, J.-L.
1978. Un cas de dimorphisme sexuel chez une ammonite carixienne *Phricodoceras taylori* (J. de C. Sowerby, 1826) Eoderoceratidae Spath, 1929. Bulletin Scientifique de Bourgogne, Dijon, vol. 31, No. 1, pp. 41–45.

Dommergues, J.-L., Ferretti, A., Géczy, B., and Mouterde, R.
1983. Eléments de corrélation entre faunes d'ammonites mésogéennes (Hongrie, Italie) et subboréales (France, Portugal) au Carixien et au Domérien inférieur. Géobios, vol. 16, No. 4, pp. 471–499, 5 text-figs, 7 pls.

Dommergues, J.-L., and Meister, C.
1990. Les faunes d'ammonites de l'Austroalpin moyen dans les Alpes Rhetiques Italiennes (region de Levigno); biostratigraphie et implications paleogeographiques. Revue de Paléobiologie, vol. 9, pp. 291–307.

Dommergues, J.-L., Meister, C., and Fauré, P.
1985. Trois espèces nouvelles d'Harpoceratinés du Carixien supérieur et du Domérier basal du Nord-Ouest de l'Europe. Les Cahiers de l'Institut Catholique de Lyon, vol. 14, pp. 153–172, 4 pls.

Dommergues, J.-L., and Mouterde, R.
1978. Les faunes d'ammonites du Carixien inférieur et moyen du gisement des Cottards (Cher). Géobios, vol. 11, No. 3, pp. 345–365, 4 text-figs., 3 pls.
1980. Modalités d'installation et d'évolution des Harpocératinés (Ammonitina) au Domérien inférieur dans sud-ouest de l'Europe (France, Portugal). Géobios, vol. 13, pp. 289–325, 6 pls.
1981. Les Acanthopleurocératinés portugais et leurs relations avec les formes subboréales. Ciências da Terra, vol. 6, pp. 77–100.
1982. *Reynesocoeloceras praeincertum* nov. sp. (Ammonitina, Carixien moyen). Remarques sur l'origine du genre Reynesocoeloceras. Géobios, vol. 15, pp. 757–763.

Dommergues, J.-L., Mouterde, R., and Phelps, M.
1984. Correlation between northwest European and Mediterranean ammonite faunas of the Pliensbachian stage, Lower Jurassic. International Symposium on Jurassic Stratigraphy, Erlangen, vol. 1, pp. 208–216, 1 table.

Dommergues, J.-L., Mouterde, R., and Rivas, P.
1984. Un faux Polymorphitiné: *Dubariceras,* nouveau genre d'Ammonitina du Carixien mesogéen. Géobios, vol. 17, No. 6, pp. 831–839, 4 text-figs., 1 pl.

Donovan, D. T.
1954. Synoptic supplement to T. Wright's "Monograph on the Lias Ammonites of the British Islands" (*1878–86*). Palaeontographical Society Monograph, vol. 107, 54 pp.
1957. Notes on the species *Cymbites laevigatus* (J. de C. Sowerby) and on the genus *Cymbites* Neumayr. Geological Magazine, vol. 94, No. 5, pp. 413–420.
1994. History of classification of Mesozoic ammonites. Journal of the Geological Society, London, vol. 151, pp. 1035–1040.

Donovan, D. T., Callomon, J. H., and Howarth, M. K.
1981. Classification of the Jurassic Ammonitina. *in* The Ammonoidea. Systematics Association, Special Volume 18, M. R. House and J. R. Senior, *eds.*, pp. 101–155.

Donovan, D. T., and Forsey, G. F.
1973. Systematics of Lower Liassic Ammonitina. University of Kansas Paleontontological Contributions, Paper 64, pp. 1–18, 4 pls.

Dubar, G., and Mouterde, R.
1978. Les formations à ammonites du Lias moyen dans le Haut Atlas de Midelt et du Tadla. Notes et Mémoires du Service Géologique, Marocco, No. 274, pp. 1–112, 11 text-figs., 6 pls.

Du Dresnay, R.
1963. Quelques ammonites de la partie inférieure du Pliensbachien (Carixien et Domérien pro parte) du jbel Bou-Rharraf (Haut Atlas oriental). Notes du Service Géologique du Maroc, vol. 23, No. 172, pp. 141–160, pls. I–II.

Dumortier, E.
1864–1869. Études paléontologiques sur les dépôts jurassiques

du bassin du Rhône, pt. I, 190 pp., 30 pls. (1864); pt. II, 254 pp., 50 pls. (1867); pt. III, 351 pp., 45 pls. (1869), Savy, Paris.

Elmi, S., Atrops, F., and Mangold, C.

1974. Les zones d'ammonites du Domérien-Callovien de l'Algérie occidentale, Pt. 1: Domérien-Toarcien. Documents de la Faculté de Sciences, Laboratoire Géologique, Lyons, No. 61, pp. 1–84, 17 text-figs., 6 pls.

Erben, H. K.

1954. Dos amonitas nuevos y su importancia para la estratigrafia del Jurásico Inferior de México. Paleontologia Méxicana, No. 1, 23 pp., 2 text-figs., 1 pl.

Fantini Sestini, N.

1962. Contributo allo Studio delle Ammoniti del Domeriano di Monte Domaro (Brescia). Rivista Italiana di Paleontologia e Stratigrafia, vol. 68, No. 4, pp. 483–554.

1974. Phylloceratina (Ammonoidea) del Pliensbachiano italiano. Rivista Italiana di Paleontologia e Stratigrafia, vol. 80, No. 2, pp. 193–250, tables 19–20.

1975. Dactylioceratidae (Ammonoidea) del Domeriano. Rivista Italiana di Paleontologia e Stratigrafia, vol. 81, No. 4, pp. 437–476, 3 tables, 4 text-figs.

1977. Hildoceratidae (Ammonoidea) della Zona a Margaritatus (Domeriano). Rivista Italiana di Paleontologia e Stratigrafia, vol. 83, No. 4, pp. 697–758, 2 text-figs., 7 pls.

1978. Il genere Phricodoceras (Polymorphytidae, Ammonoidea) nel Pliensbachiano italiano. Rivista Italiana di Paleontologia e Stratigrafia, vol. 84, No. 2, pp. 327–343, 1 table.

Feretti, A.

1972. Ricerche biostratigrafiche sul Domeriano nel Gruppo Montuoso del Nerone (Appenino Marchigiano). Rivista Italiana di Paleontologia e Stratigrafia, vol. 78, No. 1, pp. 93–130, pls. 13–18.

Fischer, R.

1971. Die Coeloceratinen (Ammonoidea) des Monte Cetona (Prov. Siena). Paläontologie, Geologie und Stratigraphie eines Profils im mediterranean Caxixium und Lotharingium. Geologica et Palaeontologica, vol. 5, pp. 93–129, pls. 1–2.

1975. Die deutschen Mittellias-Falciferen (Ammonoidea; *Protogrammoceras, Fuciniceras, Arieticeras*). Palaeontographica, Abteilung A, vol. 151, pp. 47–101.

Frebold, H.

1964a. Lower Jurassic and Bajocian ammonoid faunas of northwestern British Columbia and southern Yukon. Geological Survey of Canada, Bulletin 116, 31 pp., 8 pls.

1964b. Illustrations of Canadian fossils—Jurassic of western and Arctic Canada. Geological Survey of Canada, Paper 63–4, 106 pp., 51 pls.

1966. Upper Pliensbachian beds in the Fernie Group of Alberta. Geological Survey of Canada, Paper 66–27, 8 pp., 1 pl.

1967. Position of the Lower Jurassic genus *Fanninoceras* McLearn and the age of the Maude Formation on Queen Charlotte Islands. Canadian Journal of Earth Sciences, vol. 4, pp. 1145–1149.

1970. Pliensbachian ammonoids from British Columbia and southern Yukon. Canadian Journal of Earth Sciences, vol. 7, pp. 435–456.

1975. The Jurassic faunas of the Canadian Arctic (Lower Jurassic ammonites, biostratigraphy and correlations). Geological Survey of Canada, Bulletin 243, pp. 1–34, 5 pls.

Frebold, H., and Little, W. H.

1962. Palaeontology, stratigraphy and structure of the Jurassic rocks in Salmo map-area, British Columbia. Geological Survey of Canada, Bulletin 81, 31 pp., 5 pls.

Frebold, H., Mountjoy, E. W., and Tempelman-Kluit, D. J.

1967. New occurrences of Jurassic rocks and fossils in central and northern Yukon Territory. Geological Survey of Canada, Paper 67–12, 34 pp., 2 text-figs., 3 pls.

Fucini, A.

1896. Fauna del Lias medio del Monte Calvi presso Campiglia Marittima. Palaeontographia Italica, vol. 2, pp. 203–250, pls. 24–25.

1900–1901a. Ammoniti del Lias medio dell'Appennino centrale. Palaeontographia Italica, vol. 5 (1900 [1899]), pp. 1–42, pls. 1–6; vol. 6 (1901a [1900]), pp. 43–104, pls. 7–13.

1901b-1905. Cefalopodi Liassici del Monte di Cetona. Palaeontographia Italica, vol. 7 (1901b), pp. 1–89, pls. 1–14; vol. 10 (1904), pp. 241–264, pls. 39–42; vol. 11 (1905), pp. 265–318, pls. 43–51.

1908a. Ammoniti medoliane dell 'Appenino. Atti della Societa Toscana di Scienze Naturali Memorie, vol. 24, pp. 79–94, 1 pl.

1908b. Synopsis delle ammoniti del Medolo. Annali delle Università Toscane, vol. 28, pp. 1–107, 3 pls.

1923–1935. Fossili Domeriani dei dintorni di Taormina, Pts. 1–5. Palaeontographia Italica, vol. 26 (1923 [1920]), pp. 1–42, pls. 1–4; vol. 27 (1924 [1921]), pp. 43–64, pls. 5–8; vol. 29 (1929 [1923–28]), pp. 65–102, pls. 9–20; vol. 31 (1931 [1929–30]), pp. 103–160, pls. 21–37; vol. 35 (1935 [1934–5]), pp. 161–176, pls. 38–41.

Futterer, K.

1893. Die Ammoniten des mittleren Lias von östringen. Mitteilungen grossherzoglich badischen geologische Landesanstalt, vol. 2, pp. 277–343, pls. 8–13.

Géczy, B.

1959. *Liparoceras (Hemiparinodiceras) urkuticum* n.sg. n.sp. (Ceph.) from the Middle Liassic of the Bakony Mountains, Transdanubia, Hungary. Földtani Közlöny, vol. 89, pp. 143–147, 1 pl.

1967. Ammonoides jurassiques de Csernye, Montagne Bakony, Hongrie, pt. II (excl. Hammatoceratidae). Geologica Hungarica, Series Palaeontologica, No. 35, pp. 1–249, 65 pls.

1976. Les Ammonitines du Carixien de la Montagne du Bakony. Akadémiai Kiadó, Budapest, 223 pp., 39 pls.

Gemmellaro, G. G.

1884. Sui fossili degli strati a *Terebratula aspasia* della contrada Rocche Rosse presso Galaati (provincia di Messina). Giornale di Scienze Naturali ed Economiche, Palermo, vol. 16, pp. 167–218, pls. 1–7.

1886. Sopra taluni Harpoceratidi del Lias superioredei dintorni di Taormina. Giornale di Scienze Naturali ed Economiche, Palermo, vol. 17, pp. 109–125.

Getty, T. A.

1970. *Acanthopleuroceras* Hyatt, 1900 (Class Cephalopoda, Order Ammonoidea): proposed use of the plenary powers to designate the type-species (Jurassic). Bulletin of Zoological Nomenclature, vol. 27, pt. 2, pp. 105–109, 1 pl.

Guex, J.

1973. Aperçu biostratigraphique sur le Toarcien inférieur du Moyen Atlas marocain et discussion sur la zonation de ce sous-etage dans les séries méditerranéennes. Eclogae Geologicae Helveticae, vol. 66, pp. 493–523, pls. 1–15.

Haas, O.

1913. Die Fauna des mittleren Lias von Ballino in Südtirol. Beiträge zur Paläeontologie und Geologie Osterreich-Ungarns und des Orients, Wien, vol. 26, 161 pp., 7 pls.

Hall, R. L., and Howarth, M. K.

1983. *Protogrammoceras paltum* (Buckman), a Late Pliensbachian (Jurassic) ammonite from Axel Heiberg Island, Canadian Arctic Archipelago. Canadian Journal Earth Sciences, vol. 20, pp. 1470–1475.

Hallam, A.

1965. Observations on marine Lower Jurassic stratigraphy of North America, with special reference to the United States. Bulletin of the American Association of Petroleum Geologists, vol. 49, pp. 1485–1501, 5 text-figs.

Hallam, A., and Bradshaw, M. J.

1979. Bituminous shales and oolitic ironstones as indications of transgressions and regressions. Journal of the Geological Society of London, vol. 136, pp. 157–164.

Hauer, F. von

1861. Über die Ammoniten aus dem sogenannten Medolo der Berge Domaro und Guglielmo in Val Trompia, provinciadi Brescia. Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften, Wien, vol. 44, pp. 403–422.

Haug, E.

1885. Beiträge zu einer Monographie der Ammonitengattung *Harpoceras*. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, vol. 3, pp. 586–722, pls. 11–12.

1887. Über die "Polymorphidae", eine neue Ammoniten-familie aus dem Lias. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, vol. 2, pp. 89–163.

Hertlein, L. G.

1925. New species of marine fossil mollusca from western North America. Bulletin of the Southern California Academy of Sciences, vol. 24, pp. 39–46, pls. 3–4.

Hillebrandt, A. v.

1973a. Neue Ergebnisse über den Jura in Chile und Argentinien. Münstersche Forschungen zur Geologie und Paläontologie, vol. 31–32, pp. 167–199, 4 text-figs., 1 table.

1973b. Die Ammonitengattungen *Bouleiceras* und *Frechiella* im Jura von Chile und Argentinien. Eclogae Geologicae Helvetiae, vol. 66, pp. 351–363, 2 pls.

1981. Faunas de amonites del Liasico Inferior y Medio (Hettangiano hasta Pliensbachiano) de América del Sur (excluyendo Argentina). Cuncas sedimentarias del Jurásico y Cretácico de América del Sur, vol. 2, pp. 499–538.

1987. Liassic ammonite zones of South America and correlations with other provinces with descriptions of new genera and species of ammonites. *in* Bioestratigrafía de los sistemas regionales del Jurásico y Cretácico de América del Sur. Contributions to I.G.C.P. No. 171, Circum-Pacific Jurassic, vol 1: Jurásico anterior a los movimientos málmicos. Mendoza, Argentina, pp. 111–157, 14 pls.

1990a. Der Untere Jura im Gebiet des Rio Atuel (Provinz Mendoza, Argentinien). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, vol. 181, pp. 143–157.

1990b. Ammonites. *in* Lower Jurassic of South America and Antarctic Peninsula. by A. C. Riccardi, S. E. Damborenea, and M. O. Manceñido. Newsletters on Stratigraphy, vol. 21, pp. 94–96.

Hillebrandt, A. v., and Schmidt-Effing, R.

1981. Ammoniten aus dem Toarcium (Jura) von Chile (Südamerika). Zitteliana, vol. 6, pp. 1–74, 8 pls.

Hirano, H.

1971. Biostratigraphic study of the Jurassic Toyora Group. Memoirs of the Faculty of Science, Kyushu University, Series D, Geology, vol. 21, pp. 93–128, pls. 14–20.

1973. Biostratigraphic study of the Jurassic Toyora Group, Pt. III. Transactions and Proceedings, Palaeontological Society of Japan, N.S., No. 90, pp. 45–71, pls. 9–10.

Hoffman, K.

1968. Neue Ammonitenfunde aus dem tieferen Unter-Toarcium (Lias epsilon) des nördlichen Harzvorlandes und ihre feinstratigraphische Bedeutung. Geologisches Jahrbuch, vol. 85, pp. 1–32, 5 pls.

1982. Die Stratigraphie, Paläogeographie und Ammonitenführung des Unter-Pliensbachium (Carixium, Lias gamma) in Nordwest-Deutschland. Geologische Jahrbuch, vol. 55, Serie A, pp. 3–439, 32 text-figs., 3 tables, 40 pls.

Hoffman, K., and Martin, P. R.

1960. Die Zone des *Dactylioceras tenuicostatum* (Toarcien, Lias) in NW- und SW-Deutschland. Paläontologische Zeitschrift, vol. 34, pp. 103–149, pls. 8–12.

Howarth, M. K.

1955. Domerian of the Yorkshire Coast. Proceedings of the Yorkshire Geological Society, vol. 30, pp. 147–175, pls. 10–13.

1957. The Middle Lias of the Dorset Coast. Quarterly Journal of the Geological Society of London, vol. 113, pp. 185–203, 1 pl.

1958. A monograph of the ammonites of the Liassic family Amaltheidae in Britain. Palaeontographical Society, pt. 1, pp. i–xiv, 1–26, pls. 1–4; pt. 2, pp. xv–xxxvii, 27–53, pls. 5–10.

1973. The stratigraphy and ammonite fauna of the Upper Liassic Grey Shales of the Yorkshire Coast. Bulletin of the British Museum (Natural History), Geology, vol. 24, No. 4, pp. 237–277, 9 pls.

1992. The Ammonite family Hildoceratidae in the Lower Jurassic of Britain. Part 1. Monograph of the Palaeontographical Society, London, vol. 145, 106 pp., pls. 1–16.

Howarth, M. K., and Donovan, D. T.

1964. Ammonites of the Liassic family Juraphyllitidae in Britain. Palaeontology, vol. 7, pt. 2, pp. 286–305, 2 text-figs., pls. 48–49.

Hyatt, A.

1867. The fossil Cephalopods of the Museum of Comparative Zoology. Bulletin of the Museum of Comparative Zoology, vol 1, pp. 71–102.

1875. Remarks on two new genera of ammonites: *Agassiceras* and *Oxynoticeras*. Boston Society of Natural History, Proceedings, vol. 17, pp. 225–235.

1889. Genesis of the Arietidae. Smithsonian Contributions to Knowledge, No. 673, 238 pp.

1900. Class 5—Cephalopoda. *in* Text-book of Paleontology. C. R. Eastman, *ed.*, New York, N. Y., pp. 502–604.

I C Z N

1973. International Code of Zoological Nomenclature: Opinion 996. International Trust for Zoological Nomenclature, London, p. 23.

Imlay, R. W.

1955. Characteristic Jurassic mollusks from northern Alaska. U.S. Geological Survey Professional Paper 274-D, pp. 69–96, pls. 8–13.

1968. Lower Jurassic (Pliensbachian and Toarcian) ammonites from eastern Oregon and California. U.S. Geological Survey Professional Paper 593-C, 51 pp., 9 pls.

1981. Early Jurassic Ammonites from Alaska. U.S. Geological Survey Professional Paper 1148, 49 pp. 12 pls.

Jakobs, G. K., Smith, P. L., and Tipper, H. W.

1994a. Towards an ammonite zonation for the Toarcian of North America. Third International Jurassic Symposium, Poitiers. Géobios.

1994b. An ammonite zonation for the Toarcian (Lower Jurassic) of the North American Cordillera. Canadian Journal of Earth Sciences, vol. 31, pp. 919–942.

Jaworski, E.

1931. Über *Arnioceras geometricum* Oppel 1856 und verwandte Spezies; Nebst einem Anhang über Ammonites natrix v. Schlotheim 1820. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, vol. 65 (B), pp. 83–140, 4 text-figs., pls. 2–6.

Krumbeck, L.

1922. Zur Kenntnis des Juras der Insel Rotti. Jahrbuch Mijnwessen nederlandisch Oost-Indië, vol. 3, pp. 107–219.

Lange, W.

1932. Über ein *Hammatoceras* und einen Amaltheenvorläufer (*Proamaltheus wertheri* gen. nov. sp. nov.) aus dem Lias $\gamma + \delta$ von Werther in Westfalen. Zeitschrift der deutschen geologischen Gesellschaft, vol. 84, pp. 235–241, 7 pls.

Lehmann, U.

1968. Stratigraphie und Ammonitenführung der Ahrensburger Glazial-Gescheibe aus dem Lias epsilon (= Unt. Toarcium). Mitteilungen aus dem Geologischen Staatsinstitut in Hamburg, vol. 37, pp. 41–68, pls. 17–20.

Levi, G.

1896. Sui fossili degli strati a *Terebratula aspasia* di M. Calvi presso Campiglia. Bolletino della Società Geologica Italiana, vol. 15, pp. 262–276, 8 pls.

Lewis, P. D., and Ross, J. V.

1991. Mesozoic and Cenozoic structural history of the central Queen Charlotte Islands, British Columbia. in Evolution and hydrocarbon potential of the Queen Charlotte Basin, British Columbia. G. J. Woodsworth, ed., Geological Survey of Canada, Paper 90–10, pp. 31–50.

Matsumoto, T., and Ono, A.

1947. A biostratigraphic study of the Jurassic Toyora Group with special reference to ammonites. Science Reports of the Faculty of Science, Kyushu University, Geology, vol. 2, pp. 20–35, pls. 1–2 (in Japanese).

Mattei, J.

1967. Analyse des termes fossilifères domériens dans les Causses du sud du Massif Central français. Colloque Jurassique, Luxembourg, 44 pp.

McLearn, F. H.

1930. Notes on some Canadian Mesozoic faunas. Royal Society of Canada, Proceedings and Transactions, ser. 3, vol. 24, sect. 4, pp. 1–7, 2 pls.

1932. Contributions to the stratigraphy and paleontology of Skidegate Inlet, Queen Charlotte Islands, British Columbia. Royal Society of Canada, Proceedings and Transactions, ser. 3, vol. 26, pp. 51–80.

Meister, C.

1986. Les ammonites du Carixien des Causses (France). Mémoires suisses de Paléontologie, vol. 109, 162 pp., 23 pls.

1989. Les ammonites du Domérien des Causses (France). Centre National de la Recherche Scientifique, Paris, 80 pp., 9 pls.

Meneghini, J.

1867–1881. Monographie des fossiles du calcaire rouge ammonitique (Lias supérieur) de Lombardie et de l'Appennin Centrale. *in* Paléontologie Lombarde, A. Stoppani, *ed.*, Ser. 4, (1867), pp. 1–24, pls. 1–6; (1870), pp. 25–45, pls. 7–11, appendix pl. 1; (1874), pp. 49–80, pls. 12–16, appendix pl. 2; (1875), p. 81–104, pl. 17–20, appendix pp. 1–16, pl. 3, 4; (1876), pp. 105–112, pls. 21, 22, appendix pp. 17–40, pls. 5, 6; (1878), pp. 113–128, pls. 23–25; (1881), pp. 129–242, pls. 26–31, appendix pp. 41–56, pl. 7.

Monestier, J.

1934. Ammonites du Domérien de la région Sud-Est de l'Aveyron et de quelques régions de la Lozère à l'exclusion des Amalthéidés. Mémoires de la Société Géologique de France, N.S., vol. 10, Memoir 23, pp. 1–102, pls. 1–11.

Montfort, D. de

1808. Conchyliologie systématique et classification méthodique des Coquilles. vol. 1, pp. i–lxxxvi, 1–409, 200 pls., Paris.

Mouterde, R.

1967. Le Lias Moyen de São Pedro de Muel (Portugal), pt. 1. Comunicações dos Serviços Geológicos de Portugal, vol. 52, pp. 185–208.

1970. Le Lias Moyen de São Pedro de Muel, pt. 2, paléontologie; I, Céphalopodes. Communicaçaaes dos Serviços Geológicos de Portugal, vol. 54, pp. 39–74.

Mouterde, R., and Dommergues, J. L.

1978. Le gisement des Cottards (ou Coutards) coupe du Carixien du Cher. Bulletin d'Information des Geologues du Bassin de Paris, vol. 15, pp. 65–69, 1 pl.

Mouterde, R., Dommergues, J. L., and Rocha, R. B.

1983. Atlas des fossiles charactéristiques du Lias portugais, II: Carixien. Ciências da Terra, vol. 7, pp. 187–254.

Mouterde, R., and Rocha, R. B.

1981. Le Lias de la Région de Rio de Couros (Nord de Tomar). Sociedade Géologica de Portugal, Boletim 22, pp. 209–220, 2 pls.

Neumayr, M.

1875. Die Ammoniten der Kreide und die Systematik der Ammonitiden. Zeitschrift der Deutsche geologische Gesellschaft, vol. 27, pp. 854–892.

1878. Über unvermittelt auftretende Cephalopodentypen im Jura Mittel-Europa's. Jahrbuch der kaiserlich-königlichen geologischen Reichsanstalt, Wien, vol. 28, pp. 37–56.

Oppel, A.

1853. Der mittlere Lias schwabens neu bearbeitet. Württemberger Naturwissenschaffen Jahreshefte, Stuttgart, vol. 10, 92 pp., 4 pls.

1862. Über jurassische Cephalopoden. Paläontologische Mitteilungen, Museum königlich bayerischen Staates, vol. 1, pt. 3, pp. 127–162, pls. 40–50.

Orbigny, A. d'

1842–1851. Paléontologie française: Terrains jurassiques, pt. 1, Céphalopodes. Cosson, Masson, Paris, 642 pp., 234 pls.; (1842), pp. 1–80; (1844), pp. 193–224.

Pálfy, J., McFarlane, R. B., Smith, P. L., and Tipper, H. W.

1990. Potential for ammonite biostratigraphy of the Sinemurian part of the Sandilands Formation, Queen Charlotte Islands, British Columbia, in Current Research, Part F, Geological Survey of Canada, Paper 90–1F, pp. 47–50.

Pálfy, J., Smith, P. L., and Tipper, H. W.

1994. Sinemurian (Lower Jurassic) ammonoid biostratigraphy of the Queen Charlotte Islands, western Canada. Third International Jurassic Symposium, Poitiers. Géobios.

Parisch, C., and Viale, C.

1906. Contribuzione allo studio delle ammoniti del Lias superiore. Rivista Italiana Paleontologie, vol. 12, pp. 141–168.

Pérez, d'A., E

1982. Biostratigrafía del Jurasico de Quebrada Asientos, norte de Portrerillos, Región de Atacama. Servicio Nacional de Geologia y Mineria—Chile. Boletin 37, 149 pp.

Pia, J. V.

1913. Über eine mittelliasische Cephalopodenfauna aus dem nordöstlichen Kleinasien. Naturhistorisches Museum in Wien, Annalen, vol. 27, pp. 335–398, pls. 13–15, text-figs. 1–7.

1914. Untersuchungen über die Gattung *Oxynoticeras*. Abhandlung der kaiserlichen und königlichen geologischen Reichsanstalt, Wien, vol. 23, 179 pp., 13 pls.

Pinna, G.

1966. Nota su alcune ammoniti pliensbachiane dell'Alpe Turati (Como). Atti della Società italiana di Scienze naturali e del Museo Civico di Storia naturale di Milano, vol. 105, pp. 343–350, pl. 10.

Pinna, G., and Levi-Setti, F.

1971. I Dactylioceratidae della provincia Mediterranea (Cephalopoda, Ammonoidea). Memoirie della Società italiana di Scienze naturali e del Museo Civico di Storia naturale di Milano, vol. 19, No. 2, 136 pp.

Poulton, T. P.

1991. Hettangian through Aalenian (Jurassic) guide fossils and biostratigraphy, northern Yukon and adjacent Northwest Territories. Geological Survey of Canada, Bulletin 410, 95 pp.

Quenstedt, F. A.

1845–1849. Petrefactenkunde Deutschlands, I: Cephalopoden. Tübingen, 581 pp., 36 pls.; (1845), pp. 1–104, pls. 1–6.

1856–1858. Der Jura. Verlag der H. Laupp'shen Buchhandlung, Tübingen, 842 pp., 100 pls.; (1856), pp. 1–576, pls. 1–72.

1882–1885. Die Ammoniten des schwäbischen Jura, Vol. 1, Der schwarze Jura (Lias). Schweizerbart, Stuttgart, 440 pp., 54 pls.; (1885), pp. 241–440, pls. 31–54.

Quinzio Sinn, L. A.

1987. Stratigraphische Untersuchungen im Unterjura des Südteils der Provinz Antofagasta in Nord-Chile. Berliner Geowissenschaftliche Abhandlungen (A), vol. 78, 100 pp., 5 pls.

Repin, Y. S.

1966. Stratigrafiy i Ammonity Toarskogo Yarusa Esentral'noy chasti Omolonskogo Massiva. Materialy po Geologii i Poleznym Iskopaemym, Severo-Vostoka SSSR, Magadan, vol. 19, pp. 30–55, pls. 1–4.

1968. *in* Polevoy Atlas Yarskoy Fauny i Flory Severo-Vostoka SSSR. by A. D. Efimova, V. P. Kinasov, K. P. Paraketsov, I. V. Polubotko, Y. S. Repin, and A. S. Dagis. Ministerstvo Geologii RFSFR, Magadan, 379 pp.

1970. K voprosny o zonalinom raschlenenii toarskikh otlozhenii Severo-vostoka SSSR. Kolyma, Magadan, vol. 5, pp. 41–44.

1974. Amaltheidae from the Upper Pliensbachian of northeastern USSR and their stratigraphic significance. *in* Biostratigrafiya boreal'nogo mezozoya. V. N. Saks, *ed.*, Nauka Publishing House, Novosibirsk (in Russian).

Reynès, P.

1868. Essai de géologie et de paléontologie aveyronnaises. Baillière et Fils, Paris, 110 pp., 7 pls.

Riccardi, A. C.

1984. Las asociaciones de amonitas del Jurásico y Cretácico de la Argentina. Actas IX Congreso Geólogico Argentino 4, Buenos Aires, pp. 559–595.

Richardson, J.

1873. Report on the coal-fields of Vancouver and Queen Charlotte Islands. Geological Survey of Canada, Report of Progress for 1872–1873, pp. 32–65.

Rivas, P.

1983. El genero *Metaderoceras* (Eoderoceratacea, Ammonitina) en las Cordilleras Béticas. Estudios Geologicos, vol. 39., pp. 387–403.

Roman, F.

1938. Les ammonites jurassiques et crétacées; Essai de généra. 554 pp., 53 pls., 496 text-figs., Masson, Paris.

Rosenberg, P.

1909. Die liasische Cephalopodenfauna der Kratzalpe im Hagengebirge. Beiträge zur Paläontologie und Geologie österreich-Ungarns und des Orients, Wien, vol. 22, pp. 193–345.

Schindewolf, O. H.

1961. Die Ammoniten-Gattung *Cymbites* im deutschen Lias. Palaeontographica, Abteil A, vol. 117, pp. 193–232, pls. 29–31.

1962. Studien zur Stammesgeschichte der Ammoniten: II, Psiloceratactaceae-Eoderocerataceae. Akademie der Wissenschaften und der Literatur, Mainz, vol. 8, pp. 425–571, 91 text-figs., 1 pl.

Schlatter, R. V.

1980. Biostratigraphie und Ammonitenfauna des Unter-Pliensbachium im Typusgebiet (Pliensbach, Holzmaden und Nürtingen; Württemberg, SW.-Deutschland). Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie), vol. 65, pp. 1–251, 21 pls.

Schlegelmilch, R. S.

1976. Die Ammoniten des Süddeutschen Lias. Gustav Fischer Verlag, Stuttgart, 212 pp.

Schlotheim, E. F. v.

1820. Die Petrefactenkunde auf ihrem jetzigen Standpunkte. Gotha, 437 pp., 15 pls.

Schröder, J.

1927. Die Ammoniten der jurassischen Fleckenmergel in den Bayrischen Alpen. Palaeontographica, vol. 69, pp. 1–110, 11 pls.

Seguenza, A.

1885. I minerali della provincia di Messina. I, Rocche Messinesi, pp. 245–254.

Sey, I. I., and Kalacheva, E. D.

1980. Biostratigraphy of the Lower and Middle Jurassic deposits of the Far East. Ministry of Geology, U.S.S.R., Geological Institute, Nedra, 187 pp., 34 pls. (In Russian.)

Shimer, H. W., and Shrock, R. R.

1944. Index fossils of North America. John Wiley and Sons, New York, 837 pp.

Simpson, M.

1855. The fossils of the Yorkshire Lias. Whitby, London, 149 pp.

Smith, P. L.

1981. Biostratigraphy and ammonoid fauna of the Lower Jurassic (Sinemurian, Pliensbachian and the lowest Toarcian) of eastern Oregon and western Nevada. unpublished PhD thesis, McMaster University, 368 pp., 19 pls.

1983. The Pliensbachian ammonite *Dayiceras dayiceroides* and Early Jurassic paleogeography. Canadian Journal of Earth Sciences, vol. 20, pp. 86–91.

1986. The implications of data base management systems to paleontology: a discussion of Jurassic ammonoid data. Journal of Paleontology, vol. 60, pp. 327–340.

1988. Paleobiogeography and plate tectonics. Geoscience Canada, vol. 15, pp. 261–279.

Smith, P. L., Beyers, J., Carter, E., Jakobs, G., Pálfy, J., Pessagno, E., and Tipper, H. W.

1994. Jurassic taxa ranges and correlation charts for the Circum-Pacific: Lower Jurassic of North America. Newsletters on Stratigraphy, vol. 31, pp. 33–70.

Smith, P. L., and Tipper, H. W.

1986. Plate tectonics and paleobiogeography: Early Jurassic (Pliensbachian) endemism and diversity. Palaios, vol. 1, pp. 399–412.

1988. Biochronology, stratigraphy and tectonic setting of the Pliensbachian of Canada and the United States. *in* 2nd

International Symposium on Jurassic Stratigraphy. R. B. Rocha and A. F. Soares, *eds.*, vol. 1, Lisbon, pp. 119–138.

Smith, P. L., Tipper, H. W., and Pálfy, J.

1990. Lower Jurassic biostratigraphy of the Fannin and Ghost Creek formations, Kunga Island, British Columbia. Current Research, Part F, Geological Survey of Canada, Paper 90–1F, pp. 51–54.

Smith, P. L., Tipper, H. W., Taylor, D. G., and Guex, J.

1988. An ammonite zonation for the Lower Jurassic of Canada and the United States: the Pliensbachian. Canadian Journal of Earth Sciences, vol. 25, pp. 1503–1523.

Smith, P. L., and Westermann, G. E. G.

1990. Paleobiogeography of the ancient Pacific. Science, vol. 249, p. 680.

Sowerby, J., and Sowerby, J. de C.

1812–1846. The mineral conchology of Great Britain; or coloured figures and descriptions of those remains of testaceous animals or shells, which have been preserved at various times and depths in the earth. London, 7 vols., pls. 1–383 by J. Sowerby; pls. 384–648 by J. de C. Sowerby. vol. 2 (1818), pls. 187–203; vol. 3 (1820), pls. 254–271; vol. 4 (1821), pls. 307–318; vol. 6 (1826), pls. 504–545; vol. 6 (1827), pls. 546–580.

Spath, L. F.

1913. On Jurassic ammonites from Jebel Zaghuan (Tunisia). Quarterly Journal of the Geological Society of London, vol. 69, pp. 540–580, pls. 52–53.

1919. Notes on Ammonites. Geological Magazine, vol. 6, pp. 170–177.

1922. On Cretaceous Ammonoidea from Angola, collected by Prof. J. W. Gregory. Transactions of the Royal Society of Edinburgh, vol. 53, p. 91–160.

1923. Shales-with-Beef, a sequence in the Lower Lias of the Dorset Coast. Part II. Palaeontology. Quarterly Journal of the Geological Society of London, vol. 79, pp. 66–88.

1925. Notes on Yorkshire ammonites. The Naturalist, No. 819, pp. 107–112; No. 820, pp. 137–141; No. 821, pp. 167–172; No. 822, pp. 201–206; No. 824, pp. 263–269; No. 825, pp. 299–306; No. 826, pp. 327–331; No. 827, pp. 359–364.

1926. Notes on Yorkshire ammonites. The Naturalist, No. 829, pp. 45–49; No. 832, pp. 237–140; No. 833, pp. 169–171.

1928. On the ammonites from the Belemnite Marls. Quarterly Journal of the Geological Society of London, vol. 84, pp. 222–232, pl. 16–17.

1929. Corrections of cephalopod nomenclature. The Naturalist, pp. 269–271.

1936. The ammonites of the Green Ammonite Beds of Dorset. Quarterly Journal of the Geological Society of London, vol. 92, pp. 438–455, pls. 33.

1938. A catalogue of the ammonites of the Liassic family Liparoceratidae. British Museum of Natural History, 191 pp., 26 pls.

Suess, E.

1865. Über Ammoniten. Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften, Wien, vol. 52, pp. 71–89.

Sutherland Brown, A.

1968. Geology of the Queen Charlotte Islands, British Columbia. British Columbia Department of Mines and Petroleum Resources, Bulletin 54, 226 pp.

Thompson, R. I., Haggart, J. W., and Lewis, P. D.

1991. Late Triassic through early Tertiary evolution of the Queen Charlotte Basin, British Columbia with a perspective on hydrocarbon potential. *in* Evolution and hydrocarbon potential of the Queen Charlotte Basin, British Columbia. G. J. Woodsworth, *ed.*, Geological Survey of Canada, Paper 90–10, pp. 3–29.

Thomson, R. C., and Smith, P. L.

1992. Pliensbachian (Lower Jurassic) biostratigraphy and ammonite fauna of the Spatsizi area, north-central British Columbia. Geological Survey of Canada Bulletin 437, 87 pp.

Tipper, H. W.

1984. The age of the Jurassic Rossland Group of southeastern British Columbia. Current Research, Part A, Geological Survey of Canada, Paper 84–1A, pp. 631–632.

Tipper, H. W., Smith, P. L., Cameron, B. E. B., Carter, E. S., Jakobs, G. K., and Johns, M. J.

1991. Biostratigraphy of the Lower Jurassic formations of the Queen Charlotte Islands, British Columbia. *in* Evolution and hydrocarbon potential of the Queen Charlotte Basin, British Columbia. G. J. Woodsworth, *ed.*, Geological Survey of Canada, Paper 90–10, pp. 203–235.

Trueman, A. E.

1918. The evolution of the Liparoceratidae. Quarterly Journal of the Geological Society of London, vol. 74, pp. 247–298.

Tuchkov, I. I.

1954. Jurassic ammonites and belemnites of northeast USSR. Data on the Geology and Natural Resources of northeastern USSR, Magadan, vol. 8, pp. 98–125. (In Russian).

Vadász, M. E.

1907. Fejlödésbeli elkülönülések a Phyllocerasok családjában. Földtani Közlöny, vol. 37, pp. 349–355.

Vecchia, O.

1949. Su alcuni nomi generici di ammoniti liassici. Rivista Italiana di Paleontologia e Stratigrafia, vol. 55, pp. 139–145.

Vellutini, D., and Bustin, R. M.

1991a. Source rock potential of Mesozoic and Tertiary strata of the Queen Charlotte Islands. *in* Evolution and hydrocarbon potential of the Queen Charlotte Basin, British Columbia. G. J. Woodsworth, *ed.*, Geological Survey of Canada, Paper 90–10, pp. 381–409.

1991b. Organic maturation and source rock potential of Mesozoic and Tertiary strata, Queen Charlotte Islands, British Columbia. *in* Evolution and hydrocarbon potential of the Queen Charlotte Basin, British Columbia. G. J. Woodsworth, *ed.*, Geological Survey of Canada, Paper 90–10, pp. 411–451.

Venzo, S.

1952. Nuove fauna ad Ammoniti del Domeriane-Aaleniano del'Alpe Turati e dintomi (Alta Brianza). Atti della Società Italiana di Scienza Naturali, Milano, vol. 91, pp. 95–123, 2 pls.

Westermann, G. E. G., ed.

1992. The Jurassic of the Circum-Pacific. Cambridge University Press, Cambridge, 676 pp.

Whiteaves, J. F.

1884. On the fossils of the coal-bearing deposits of the Queen Charlotte Islands collected by Dr. G. M. Dawson in 1878. Geological and Natural History Survey of Canada, Mesozoic Fossils, vol. 1, pt. 3, pp. 1–262, pls. 21–32.

1900. On some additional or imperfectly understood fossils from the Cretaceous rocks of the Queen Charlotte Islands, with a revised list of species from these rocks. Geological Survey of Canada, Mesozoic fossils, vol. 1, pt. 4, pp. 263–307, pls. 33–39.

Wiedenmayer, F.

1977. Die Ammoniten des Besazio-Kalks (Pliensbachian, Südtessin). Schweizerische Paläontologische Abhandlungen, vol. 98, pp. 1–169, 19 pls.

1980. Die Ammoniten der mediterranen Provinz im Pliensbachian und unteren Toarcian aufgrund neuer Untersuchungen im Generoso-Becken (Lombardische Alpen). Denkschriften der Schweizerischen Naturforschenden Gesellschaft, vol. 93, 260 pp., 32 pls.

Woodsworth, G. J., ed.

1991. Evolution and hydrocarbon potential of the Queen Charlotte Basin, British Columbia. Geological Survey of Canada, Paper 90–10, 569 pp.

Wright, T.

1878–1886. A monograph on the Lias ammonites of the British Islands. Monographs of the Palaeontographical Society, part 3 (1880), pp. 165–264, pls. 19–40; part 5 (1882), pp. 329–400, pls. 49–69; part 7 (1884), pp. 441–480, pls. 78–87.

Young, G., and Bird, J.

1828. A geological survey of the Yorkshire Coast: describing the strata and fossils occurring between the Humber and the Tees, from the German Ocean to the Plain of York. 2nd ed., Whitby, London, 368 pp., 17 pls.

Zieten, C. H.

1830. Die Versteinerungen Württembergs. Schweizerbart, Stuttgart, pp. 1–16, pls. 1–12.

1832. Die Versteinerungen Württembergs. Schweizerbart, Stuttgart, pp. 33–64, pls. 25–48.

Zittel, K. A. v.

1884. Handbuch der Paläontologie. Cephalopoda, vol. 1, pt. 2, Munich, pp. 329–522.

PLATES

EXPLANATION OF PLATE 1

Figures are natural size unless otherwise indicated. The last suture is marked by an arrowhead.

Figure Page

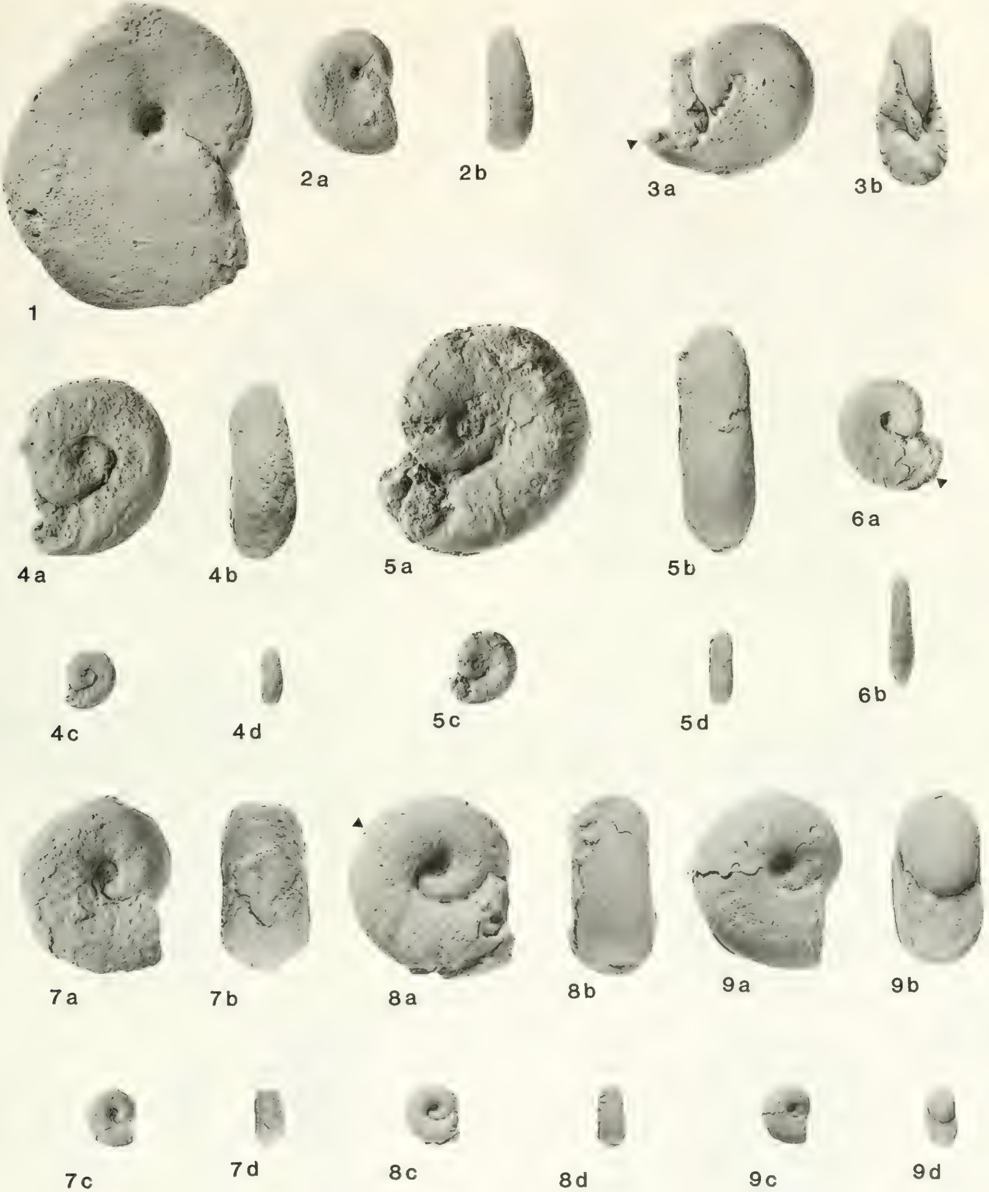
1. *Phylloceras bonarellii* Bettoni, 1900. 19
Hypotype: GSC 98693; Locality: D08 (GSC Loc. O-93564); Ghost Creek Formation, Whiteavesi Zone.

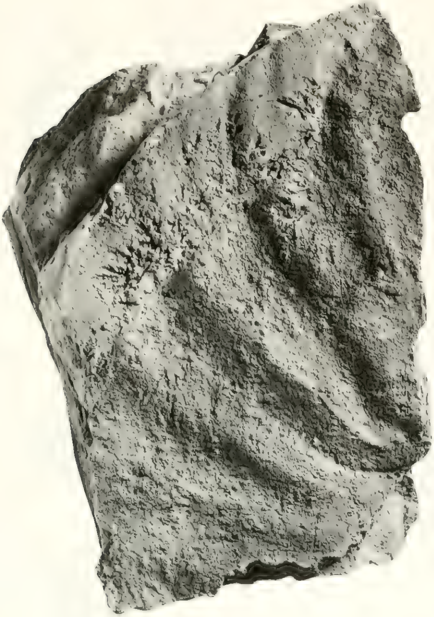
2,3. *Phylloceras* sp. 20
2a,b. Specimen: GSC 98574; Locality: E55 (GSC Loc. O-91827); Fannin Formation, Kunae Zone.
3a,b. Specimen: GSC 98575; Locality: ET1 (GSC Loc. O-93743); Fannin Formation, Kunae Zone.

4,5. *Cymbites laevigatus* (J. de C. Sowerby, 1827). 24
4a-d. Hypotype: GSC 98580, a,b ×3; Locality: I14 (GSC Loc. C-81730); Fannin Formation, Kunae Zone.
5a-d. Hypotype: GSC 98579, a,b ×3; Locality: ET4 (GSC Loc. O-13628); Fannin Formation, Kunae Zone.

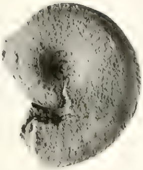
6. *Tragophylloceras* new species? 21
6a,b. Specimen: GSC 98581; Locality: ET4 (GSC Loc. O-93741); Fannin Formation, Kunae Zone.

7–9. *Cymbites centriglobus* (Oppel, 1862) 23
7a-d. Hypotype: GSC 98576, a,b ×3; Locality: ET4 (GSC Loc. O-13628); Fannin Formation, Kunae Zone.
8a-d. Hypotype: GSC 98577, a,b ×3; Locality: ET4 (GSC Loc. O-13628); Fannin Formation, Kunae Zone.
9a-d. Hypotype: GSC 98578, a,b ×3; Locality: ET4 (GSC Loc. O-48573); Fannin Formation, Kunae Zone.

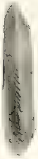

1
2a
2b
3a
3b
4a
4b
5a
5b
6a
4c
4d
5c
5d
6b
7a
7b
8a
8b
9a
9b
7c
7d
8c
8d
9c
9d



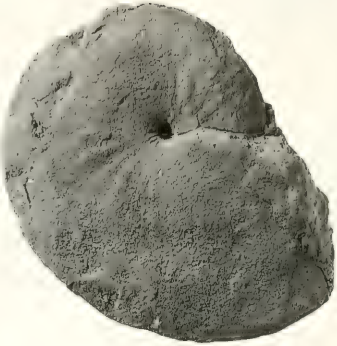
1



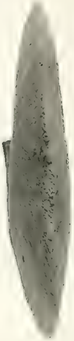
2a



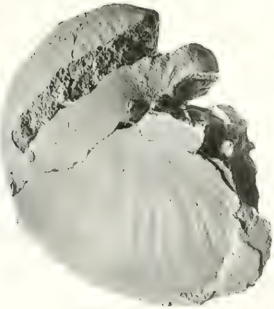
2b



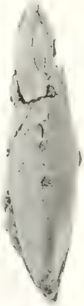
3a



3b

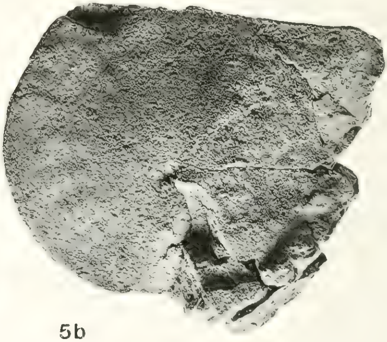


4a

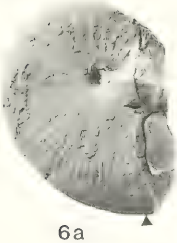


4b

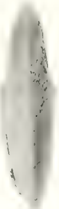
5a



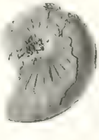
5b



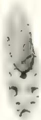
6a



6b



7a



7b

EXPLANATION OF PLATE 2

All figures are natural size. The last suture is marked by an arrowhead.

Figure Page

1. *Gleviceras*? sp. 33
   Specimen: GSC 98582; Locality: I02 (GSC Loc. O-93721); Rennell Junction Member, Whiteavesi Zone.
2. *Fanninoceras* (*Fanninoceras*) *bodegae* McLearn, 1932. 27
   2a,b. Holotype: GSC 6518; Locality: ET4 (GSC Loc. C-117032); Fannin Formation, Kunae Zone.

3–7. *Fanninoceras* (*Fanninoceras*) *carlottense* McLearn, 1930. 28
   3a,b. Holotype: GSC 4878; Locality: ET5 (GSC Loc. C-117031); Fannin Formation, Carlottense Zone.
   4a,b. Hypotype: GSC 98585; Locality: ET5 (GSC Loc. C-80834); Fannin Formation, Carlottense Zone.
   5a,b. Hypotype: GSC 98586; Locality: ET5 (GSC Loc. C-80831); Fannin Formation, Carlottense Zone.
   6a,b. Hypotype: GSC 87807; Locality: ET5 (GSC Loc. C-117031); Fannin Formation, Carlottense Zone.
   7a,b. Hypotype: GSC 98600; Locality: E63 (GSC Loc. O-93750); Fannin Formation, Carlottense Zone.

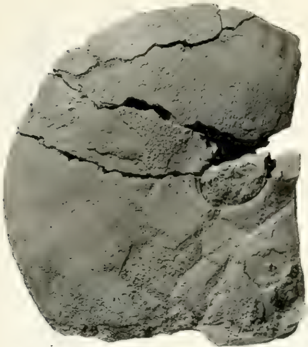
EXPLANATION OF PLATE 3

All figures are natural size. The last suture is marked by an arrowhead.

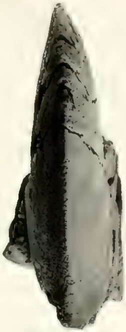
Figure Page

1–12. *Fanninoceras* (*Fanninoceras*) *fannini* McLearn, 1930. 29

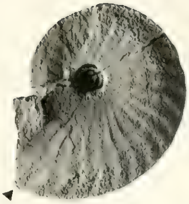
1a,b. Plesiotype of McLearn (1932): GSC 6495; Locality: ET4 (GSC Loc. C-117032); Fannin Formation, Kunae Zone.
2a,b. Holotype: GSC 9054; Locality: ET4 (GSC Loc. C-117032); Fannin Formation, Kunae Zone.
3a,b. Holotype of *F. dolmagii* McLearn, 1932: GSC 6519; Locality: ET4 (GSC Loc. C-117034); Fannin Formation, Kunae Zone.
4a,b. Plesiotype of McLearn (1932): GSC 6494; Locality: ET4 (GSC Loc. C-117032); Fannin Formation, Kunae Zone.
5. Hypotype: GSC 98594; Locality: ET4 (GSC Loc. O-13628); Fannin Formation, Kunae Zone.
6a,b. Plesiotype of McLearn (1932): GSC 6493; Locality: ET4 (GSC Loc. C-117032); Fannin Formation, Kunae Zone.
7a,b. Hypotype: GSC 98596; Locality: GT4 (GSC Loc. C-81927); Fannin Formation, Kunae Zone.
8. Hypotype: GSC 98597; Locality: ET4 (GSC Loc. C-80839); Fannin Formation, Kunae Zone.
9. Hypotype: GSC 98598; Locality: ET5 (GSC Loc. C-80814); Fannin Formation, Carlottense? Zone.
10. Hypotype: GSC 87799; Locality: GT4 (GSC Loc. C-81927); Fannin Formation, Kunae Zone.
11a,b. Hypotype: GSC 98588; Locality: E63 (GSC Loc. O-93750); Fannin Formation, Carlottense Zone.
12a,b. Hypotype: GSC 98694; Locality: ET5 (GSC Loc. C-80832); Fannin Formation, Carlottense Zone.



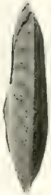
1a



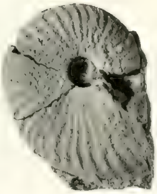
1b



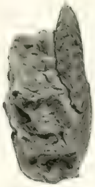
2a



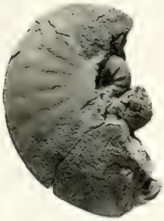
2b



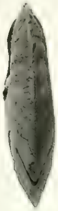
3a



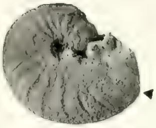
3b



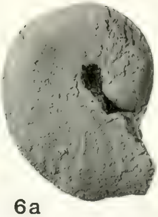
4a



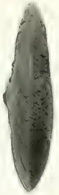
4b



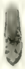
5



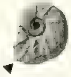
6a



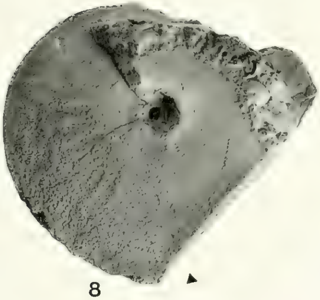
6b



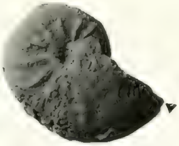
7a



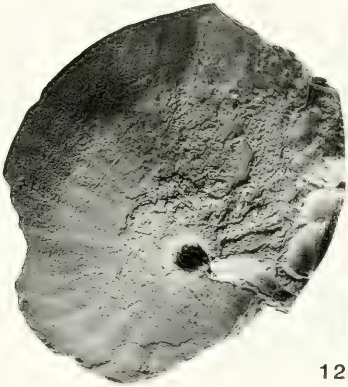
7b



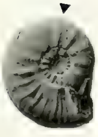
8



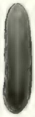
9



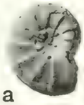
10



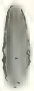
11a



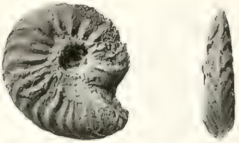
11b



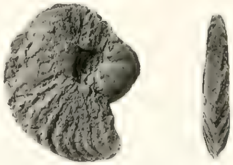
12a



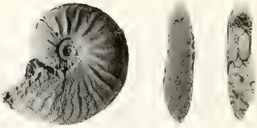
12b



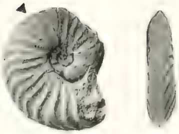
1a 1b



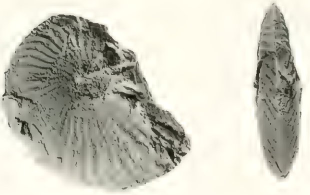
2a 2b



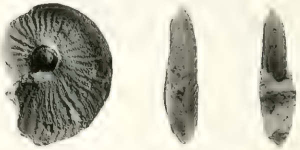
3a 3b 3c



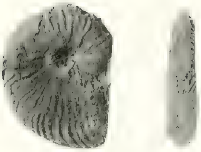
4a 4b



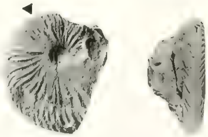
5a 5b



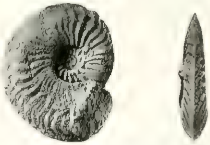
6a 6b 6c



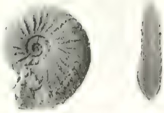
7a 7b



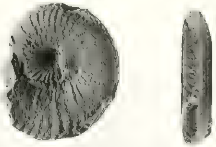
8a 8b



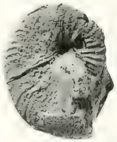
9a 9b



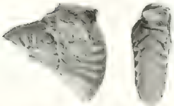
10a 10b



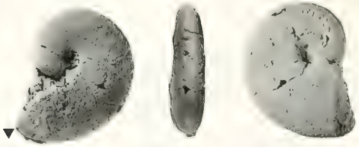
11a 11b



12



13a 13b



14a 14b 14c

EXPLANATION OF PLATE 4

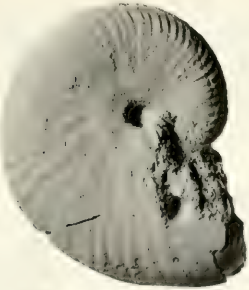
All figures are natural size. The last suture is marked by an arrowhead.

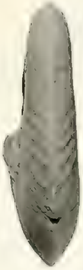
Figure		Page
1–4.	*Fanninoceras* (*Fanninoceras*) *crassum* McLearn, 1932.	28
	1a,b. Paratype: GSC 6517; Locality: ET4 (GSC Loc. C-117032); Fannin Formation, Kunae Zone.	
	2a,b. Holotype: GSC 6496; Locality: ET4 (GSC Loc. C-117032); Fannin Formation, Kunae Zone.	
	3a-c. Hypotype: GSC 98603; Locality: GT4 (GSC Loc. C-81927); Fannin Formation, Kunae Zone.	
	4a,b. Hypotype: GSC 87798; Locality: ET4 (GSC Loc. O-48573); Fannin Formation, Kunae Zone.	
5–8,11,12.	*Fanninoceras* (*Fanninoceras*) *kunae* McLearn, 1930.	30
	5a,b. Plesiotype of McLearn (1932): GSC 6670; Locality: ET4 (GSC Loc. C-117034); Fannin Formation, Kunae Zone.	
	6a-c. Holotype: GSC 4876c; Locality: ET4 (GSC Loc. C-117034); Fannin Formation, Kunae Zone.	
	7a,b. Hypotype: GSC 98607; Locality: E55 (GSC Loc. O-91827); Fannin Formation, Kunae Zone.	
	8a,b. Hypotype: GSC 98608; Locality: ET4 (GSC Loc. C-81724); Fannin Formation, Kunae Zone.	
	11a,b. Holotype of *F. lowrii* McLearn, 1930: GSC 9055; Locality: ET4 (GSC Loc. C-117034); Fannin Formation, Kunae Zone.	
	12. Hypotype: GSC 98612; Locality: I06 (GSC Loc. C-90542); Fannin Formation, Kunae Zone.	
9,10.	*Fanninoceras* (*Fanninoceras*) *latum* McLearn, 1930.	31
	9a,b. Holotype: GSC 9058; Locality: ET4 (GSC Loc. C-117032); Fannin Formation, Kunae Zone.	
	10a,b. Hypotype: GSC 98610; Locality: ET4 (GSC Loc. C-80839); Fannin Formation, Kunae Zone.	
13.	*Fanninoceras* (*Fanninoceras*) sp. 1.	31
	13a,b. Specimen: GSC 98589; Locality: ET5 (GSC Loc. C-117005); Fannin Formation, Carlottense Zone.	
14.	*Fanninoceras* (*Fanninoceras*) sp. 2.	32
	14a-c. Specimen: GSC 98613; Locality: E63 (GSC Loc. C-90545); Fannin Formation, Carlottense Zone.	

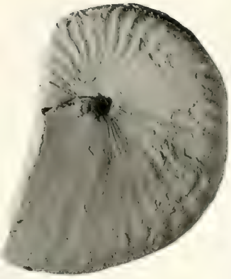
EXPLANATION OF PLATE 5

All figures are natural size.

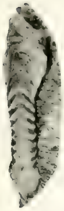
Figure		Page
1,2.	*Fanninoceras* (*Fanninoceras*) *fannini* McLearn, 1930.	29
	1a,b. Hypotype: GSC 99030; Locality: I07 (GSC Loc. C-177355); Fannin Formation, Kunae Zone.	
	2a,b. Hypotype: GSC 99031; Locality: I07 (GSC Loc. C-177355); Fannin Formation, Kunae Zone.	
3–12.	*Oistoceras compressum*, new species.	53
	3a,b. Paratype: GSC 98625; Locality: ET3 (GSC Loc. C-80840); Rennell Junction Member, Whiteavesi or Freboldi Zone.	
	4a,b. Paratype: GSC 98696; Locality: FT1 (GSC Loc. C-156675); Rennell Junction Member, Freboldi Zone.	
	5a,b. Holotype: GSC 99039; Locality: FT1 (GSC Loc. C-177370); Rennell Junction Member, Whiteavesi or Freboldi Zone.	
	6a,b. Paratype: GSC 98710; Locality: FT1 (GSC Loc. C-156675); Rennell Junction Member, Freboldi Zone.	
	7a,b. Paratype: GSC 98738; Locality: FT1 (GSC Loc. C-156675); Rennell Junction Member, Freboldi Zone.	
	8a,b. Paratype: GSC 99027; Locality: FT1 (GSC Loc. C-156675); Rennell Junction Member, Freboldi Zone.	
	9a,b. Paratype: GSC 99038; Locality: FT1 (GSC Loc. C-156675); Rennell Junction Member, Freboldi Zone.	
	10a,b. Paratype: GSC 99041; Locality: FT1 (GSC Loc. C-156675); Rennell Junction Member, Freboldi Zone.	
	11a,b. Paratype: GSC 99042; Locality: FT1 (GSC Loc. C-156675); Rennell Junction Member, Freboldi Zone.	
	12a,b. Paratype: GSC 99043; Locality: FT1 (GSC Loc. C-156675); Rennell Junction Member, Freboldi Zone.	
13–15.	*Fanninoceras* (*Charlotticeras*) *carteri*, new species.	32
	13a,b. Paratype: GSC 99029; Locality: I07 (GSC Loc. C-177355); Fannin Formation, Kunae Zone.	
	14a,b. Paratype: GSC 99028; Locality: I07 (GSC Loc. C-177355); Fannin Formation, Kunae Zone.	
	15a,b. Paratype: GSC 99026; Locality: I07 (GSC Loc. C-177355); Fannin Formation, Kunae Zone.	

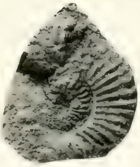

1a

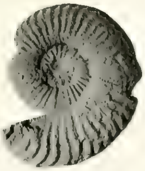

1b

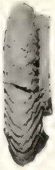

2a

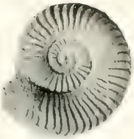
2b

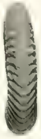

3a

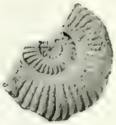

3b

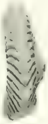

4a

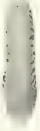

4b

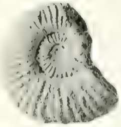

5a

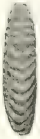

5b

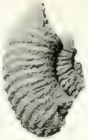

6a

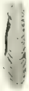

6b

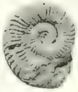

7a


7b

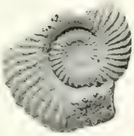

8a

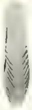

8b

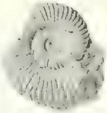

9a

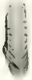

9b

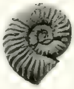
10a

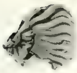

10b

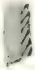

11a

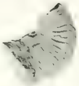

11b

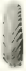

12a

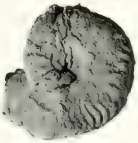

12b

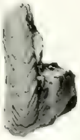

13a

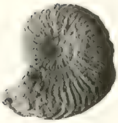

13b


14a

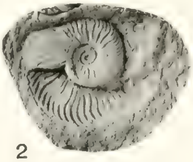

14b

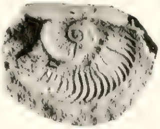

15a

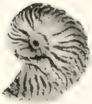

15b

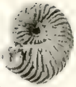

1a

1b

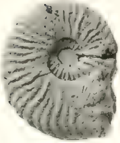

2


3

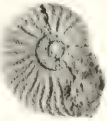

4


5a

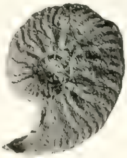
5b


6a

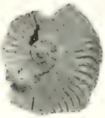
6b


7a

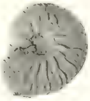
7b

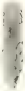

8a

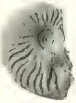
8b


9a

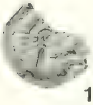
9b

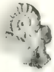

10a

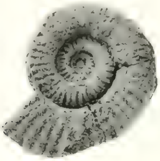

10b


11a

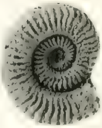
11b


12


14


15

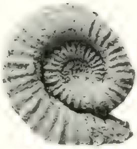
16a

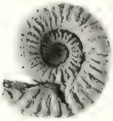

16b

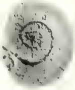
13a

13b

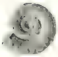
17a


17b

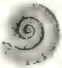

18


19a

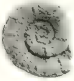
19b

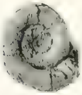

20a

20b


21a

21b


22


23

EXPLANATION OF PLATE 6

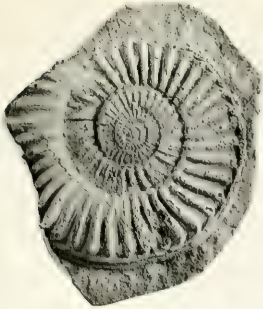
All figures are natural size.

Figure		Page
1–5.	*Fanninoceras* (*Charlotticeras*) *carteri*, new species.	32
1a,b.	Holotype: GSC 98614; Locality: E57 (GSC Loc. C-80234); Fannin Formation, Kunae Zone.	
2.	Paratype: GSC 98615 (latex cast); Locality: E57 (GSC Loc. C-80234); Fannin Formation, Kunae Zone.	
3.	Paratype: GSC 98616 (latex cast); Locality: E57 (GSC Loc. C-80234); Fannin Formation, Kunae Zone.	
4.	Paratype: GSC 98617; Locality: E57 (GSC Loc. C-80234); Fannin Formation, Kunae Zone.	
5a,b.	Paratype: GSC 98618; Locality: I14 (GSC Loc. C-81730); Fannin Formation, Kunae Zone.	
6–11.	*Fanninoceras* (*Charlotticeras*) *maudense*, new species.	32
6a,b.	Paratype: GSC 98619; Locality: D20 (GSC Loc. C-80765); Fannin Formation, Kunae Zone.	
7a,b.	Holotype: GSC 98620; Locality: D20 (GSC Loc. C-80765); Fannin Formation, Kunae Zone.	
8a,b.	Paratype: GSC 98621; Locality: I06 (GSC Loc. C-90542); Fannin Formation, Kunae Zone.	
9a,b.	Paratype: GSC 98622; Locality: ET4 (GSC Loc. O-93741); Fannin Formation, Kunae Zone.	
10a,b.	Paratype: GSC 98623; Locality: E56 (GSC Loc. C-80233); Fannin Formation, Kunae Zone.	
11a,b.	Paratype: GSC 98624; Locality: E57 (GSC Loc.C-80234); Fannin Formation, Kunae Zone.	
12–14.	*Gemmellaroceras* sp.	34
12.	Specimen: GSC 99024; Locality: FT1 (GSC Loc. C-177370); Rennell Junction Member, Freboldi Zone.	
13a,b.	Specimen: GSC 99022; Locality: FT1 (GSC Loc. C-177370); Rennell Junction Member, Freboldi Zone.	
14.	Specimen: GSC 99023; Locality: FT1 (GSC Loc. C-177370); Rennell Junction Member, Freboldi Zone.	
15–18.	*Polymorphites confusus* (Quenstedt, 1856).	35
15.	Hypotype: GSC 98626; Locality: B04 (GSC Loc. C-117019); Rennell Junction Member, Whiteavesi Zone.	
16a,b.	Hypotype: GSC 98627; Locality: B04 (GSC Loc. C-117019); Rennell Junction Member, Whiteavesi Zone.	
17a,b.	Hypotype: GSC 98628; Locality: B04 (GSC Loc. C-117019); Rennell Junction Member, Whiteavesi Zone.	
18.	Hypotype: GSC 98629; Locality: B04 (GSC Loc. C-117019); Rennell Junction Member, Whiteavesi Zone.	
19–23.	*Gemmellaroceras aenigmaticum* (Gemmellaro, 1884).	34
19a,b.	Hypotype: GSC 98630; Locality: B04 (GSC Loc. C-117019); Rennell Junction Member, Whiteavesi Zone.	
20a,b.	Hypotype: GSC 98631; Locality: ET1 (GSC Loc. O-48603).	
21a,b.	Hypotype: GSC 98632; Locality: ET1 (GSC Loc. O-48603).	
22.	Hypotype: GSC 98633; Locality: B04 (GSC Loc. C-117019); Rennell Junction Member, Whiteavesi Zone.	
23.	Hypotype: GSC 95575; Locality: B04 (GSC Loc. C-117019); Rennell Junction Member, Whiteavesi Zone.	

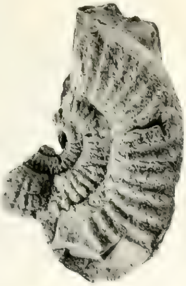
EXPLANATION OF PLATE 7

All figures are natural size. The last suture is marked by an arrowhead.

Figure		Page
1–5.	*Acanthopleuroceras thomsoni*, new species.	36
	1a,b. Paratype: GSC 98635 (latex cast); Locality: GT3 (GSC Loc. C-118697); Rennell Junction Member.	
	2a,b. Paratype: GSC 98636; Locality: B04 (GSC Loc. C-117019); Rennell Junction Member, Whiteavesi Zone.	
	3a,b. Paratype: GSC 98637; Locality: B04 (GSC Loc. C-117019); Rennell Junction Member, Whiteavesi Zone.	
	4a,b. Holotype: GSC 98638; Locality: GT3 (GSC Loc. C-81712); Rennell Junction Member.	
	5a,b. Paratype: GSC 98639; Locality: B04 (GSC Loc. C-117019); Rennell Junction Member, Whiteavesi Zone.	
6–10.	*Acanthopleuroceras whiteavesi* Smith and Tipper, 1988.	36
	6a,b. Paratype: GSC 87791; Locality: E27 (GSC Loc. O-91794); Rennell Junction Member, Whiteavesi Zone.	
	7a,b. Holotype: GSC 87790; Locality: E27 (GSC Loc. O-91794); Rennell Junction Member, Whiteavesi Zone.	
	8a,b. Hypotype: GSC 87811; Locality: ET1 (GSC Loc. C-80836).	
	9a,b. Hypotype: GSC 87810; Locality: ET1 (GSC Loc. O-48603).	
	10a,b. Hypotype: GSC 98653; Locality: E27 (GSC Loc. O-91794); Rennell Junction Member, Whiteavesi Zone.	

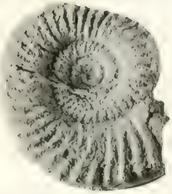


1



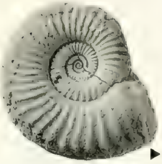
2

3a



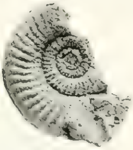
3b

4a



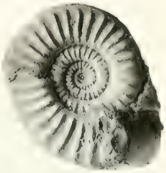
4b

5a



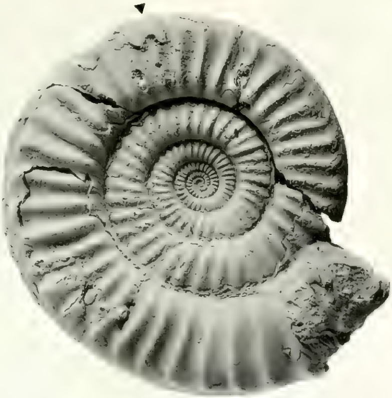
5b

6a

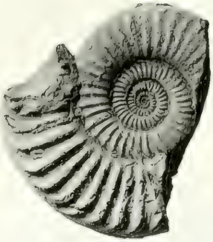


6b

7a

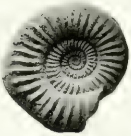


7b



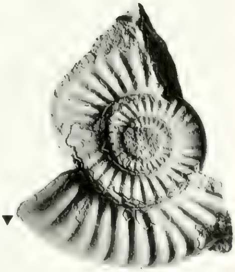
8

9a

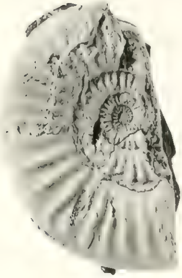


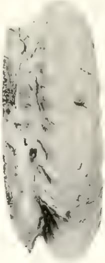
9b

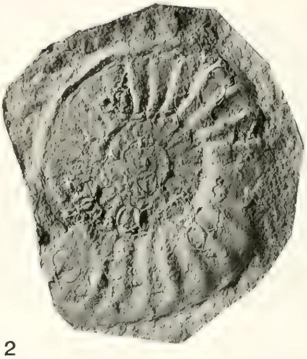
10a

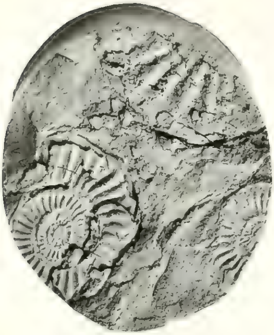


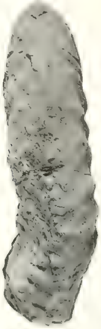
10b

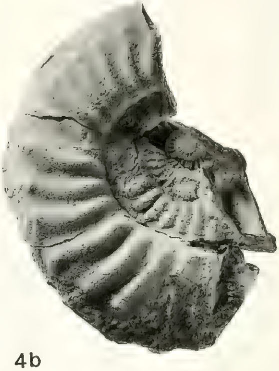

1a

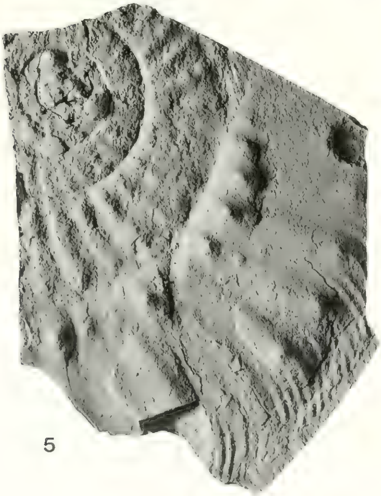

1b

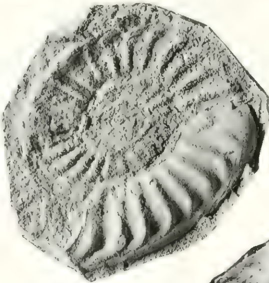

2

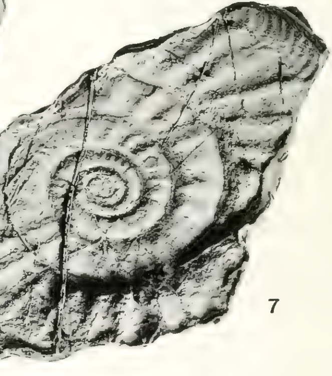

3


4a


4b


5


6


7

EXPLANATION OF PLATE 8

All figures are natural size.

Figure — Page

1–3,6. *Tropidoceras actaeon* (d'Orbigny, 1844). 37

1a,b. Hypotype: GSC 98645; Locality: D11 (GSC Loc. C-80755); Ghost Creek Formation, Whiteavesi Zone.

2. Hypotype: GSC 98646 (latex cast); Locality: G05 (GSC Loc. C-90580); Ghost Creek Formation, Whiteavesi Zone.

3. Hypotype: GSC 98647; Well core sample: H05 (GSC Loc. C-90642); Ghost Creek Formation, Whiteavesi Zone.

6. Hypotype: GSC 98695 (latex cast); Locality: D07 (GSC Loc. C-80249); Ghost Creek Formation, Whiteavesi Zone.

4. *Tropidoceras* new species 1. 40

4a,b. Specimen: GSC 98648; Locality: E34 (GSC Loc. O-91814); Rennell Junction Member, Whiteavesi Zone.

5. *Tropidoceras flandrini obtusa* (Futterer, 1893). 38

Hypotype: GSC 98699; Locality: I08 (GSC Loc. C-90974); Ghost Creek Formation, Imlayi Zone.

7. *Tropidoceras* aff. *rursicosta* (Buckman, 1918). 39

Specimen: GSC 98650 (latex cast); Locality: E01 (GSC Loc. C-80241); Ghost Creek Formation, Imlayi Zone.

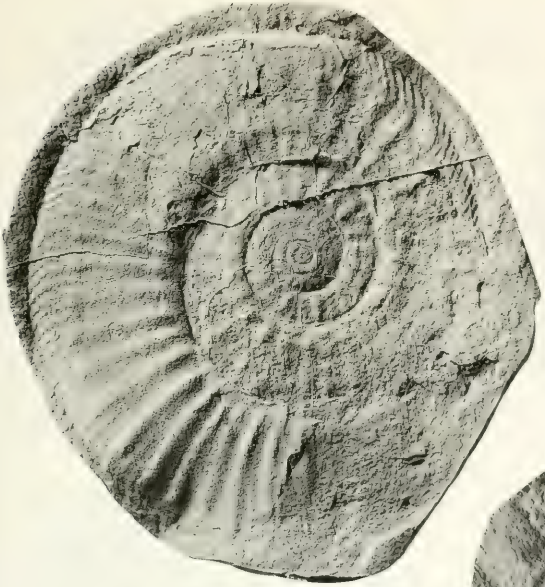
EXPLANATION OF PLATE 9

All figures are natural size.

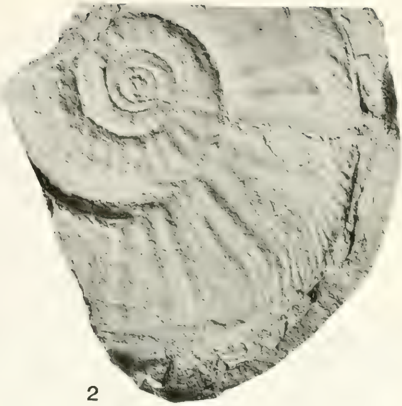
Figure Page

1–2,4. *Tropidoceras flandrini flandrini* (Dumortier, 1869). 38
   1. Hypotype: GSC 87793 (latex cast); Locality: I08 (GSC Loc. C-90977); Ghost Creek Formation, Imlayi Zone;
   2. Hypotype: GSC 98652 (latex cast); Locality: I08 (GSC Loc. C-90977); Ghost Creek Formation, Imlayi Zone.
   4. Hypotype: GSC 95574; Locality: I08 (GSC Loc. C-90977); Ghost Creek Formation, Imlayi Zone.

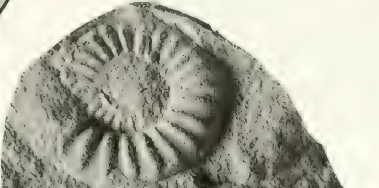
3,5. *Tropidoceras flandrini obtusa* (Futterer, 1893). 38
   3a,b. Hypotype: GSC 99044 (a = latex cast); Locality: D08 (GSC Loc. O-93564); Ghost Creek Formation, Whiteavesi Zone.
   5. Hypotype: GSC 98654 (latex cast); Locality: D08 (GSC Loc. O-93564); Ghost Creek Formation, Whiteavesi Zone.



1

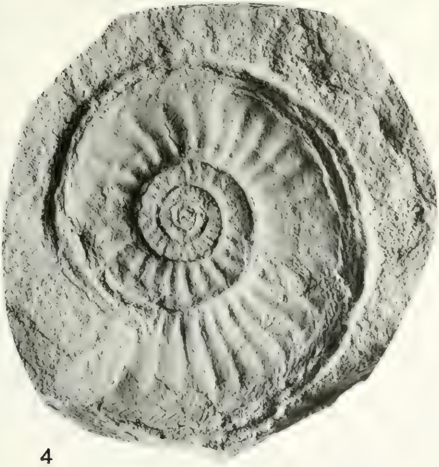


2

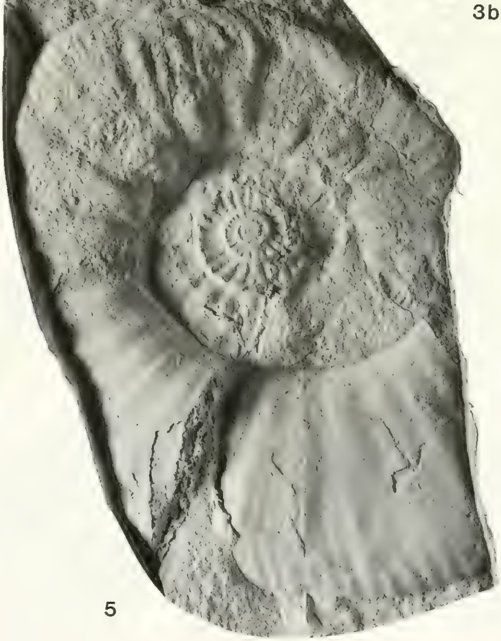


3a

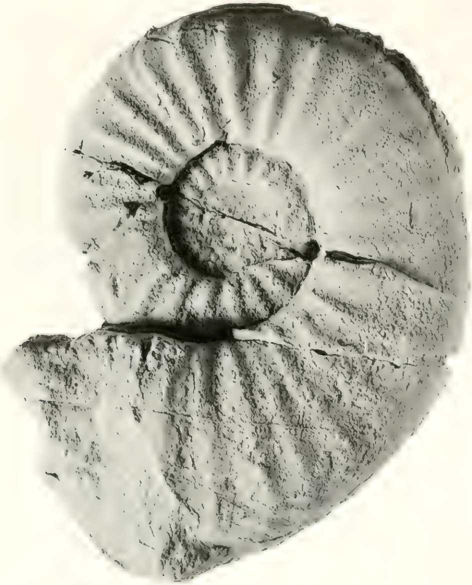
3b

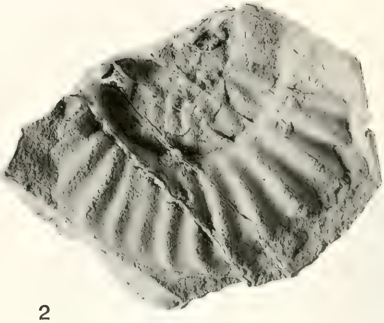


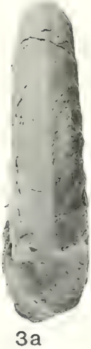
4

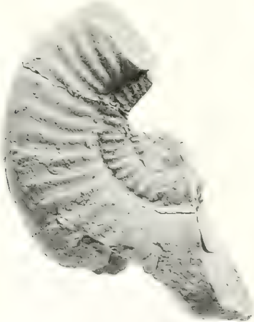


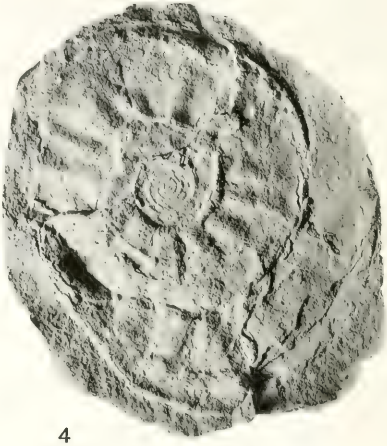
5

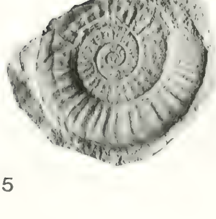

1

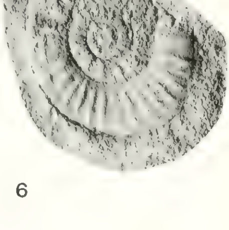

2

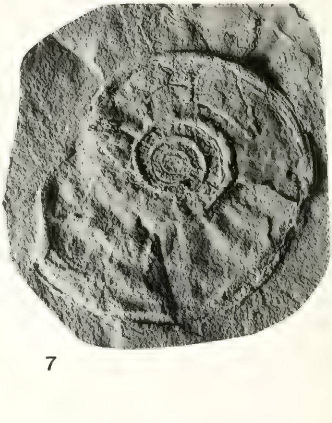

3a


3b


4


5


6


7

EXPLANATION OF PLATE 10

All figures are natural size.

Figure — Page

1,2. *Tropidoceras masseanum rotunda* (Futterer, 1893). 39
  1. Hypotype: GSC 95573; Locality: D11 (GSC Loc. O-93575); Ghost Creek Formation, Whiteavesi Zone.
  2. Hypotype: GSC 98656 (latex cast); Locality: D06 (GSC Loc. C-80246); Ghost Creek Formation, Whiteavesi Zone.

3. *Tropidoceras* new species 2. 40
  3a,b. Specimen: GSC 98657; Locality: ET1 (GSC Loc. C-80836).

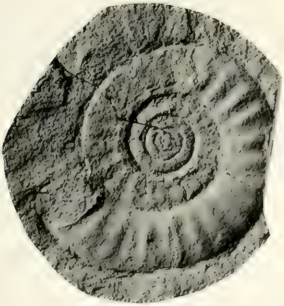
4,7. *Tropidoceras* cf. *erythraeum* (Gemmellaro, 1884). 38
  4. Specimen: GSC 98658 (latex cast); Locality: G01 (GSC Loc. C-90978); Ghost Creek Formation, Imlayi Zone.
  7. Specimen: GSC 87788 (latex cast); Locality: G02 (GSC Loc. C-90556); Ghost Creek Formation, Imlayi Zone.

5,6. *Gemmellaroceras* cf. *alloplocum* (Gemmellaro, 1884). 34
  5. Specimen: GSC 98659 (latex cast); Locality: G03 (GSC Loc. C-90547); Ghost Creek Formation, Imlayi Zone.
  6. Specimen: GSC 98660; Locality: E13 (GSC Loc. C-80329); Ghost Creek Formation, Imlayi Zone.

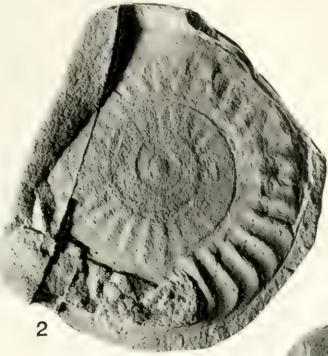
EXPLANATION OF PLATE 11

All figures are natural size.

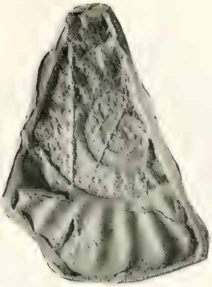
Figure		Page
1–3.	*Tropidoceras* species 1.	40
	1. Specimen: GSC 98662; Locality: I08 (GSC Loc. C-90977); Ghost Creek Formation, Imlayi Zone.	
	2. Specimen: GSC 98663 (latex cast); Locality: G01 (GSC Loc. C-90549); Ghost Creek Formation, Imlayi Zone.	
	3. Specimen: GSC 98664 (latex cast); Locality: E20 (GSC Loc. O-91803); Rennell Junction Member, Whiteavesi Zone.	
4–6.	*Miltoceras* aff. *sellae* (Gemmellaro, 1884).	42
	4. Specimen: GSC 98665; Locality: E14 (GSC Loc. C-80330); Ghost Creek Formation, Imlayi Zone.	
	5. Specimen: GSC 98666; Locality: G01 (GSC Loc. C-81926); Ghost Creek Formation, Imlayi Zone.	
	6. Specimen: GSC 98667; Locality: ET1 (GSC Loc. O-93577).	
7,8.	*Reynesocoeloceras* spp.	50
	7. Specimen: GSC 98668 (latex cast); Locality: GT1 (GSC Loc. C-90579); Rennell Junction Member.	
	8. Specimen: GSC 98669; Locality: E40 (GSC Loc. C-80350); Rennell Junction Member, Whiteavesi Zone.	



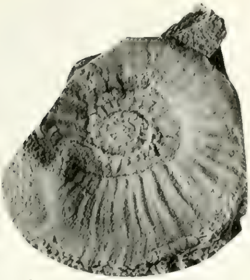
1



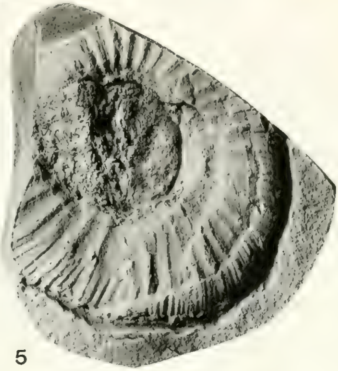
2



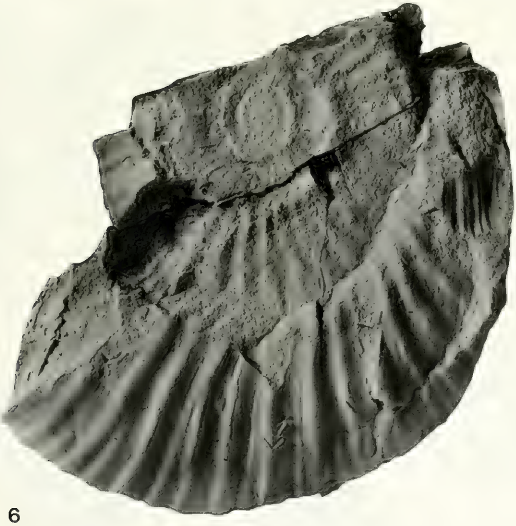
3



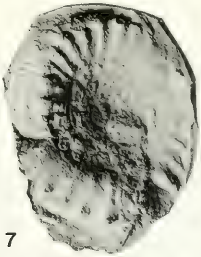
4



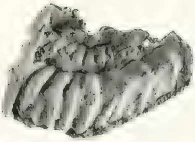
5



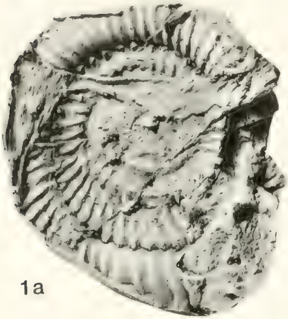
6

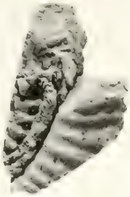


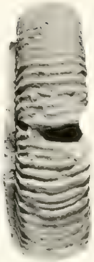
7

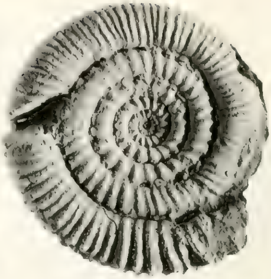


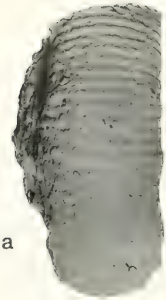
8

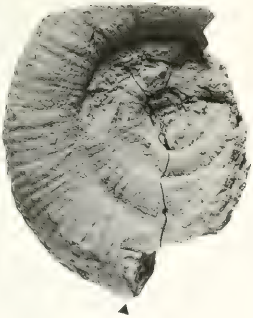

1a

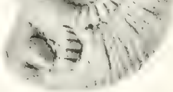

1b

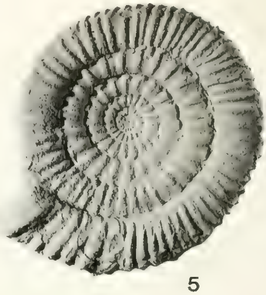

2a

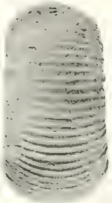

2b

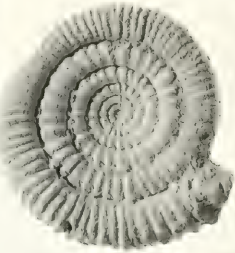

3a


3b

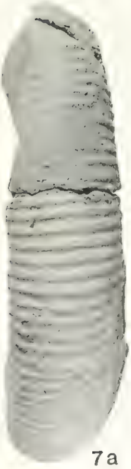

4a

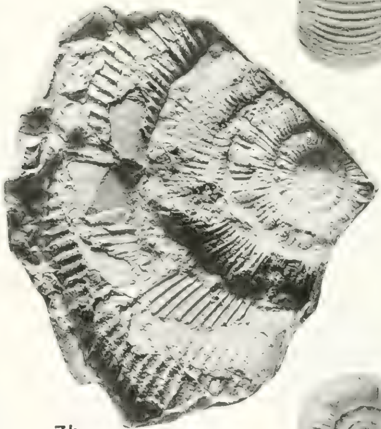

5

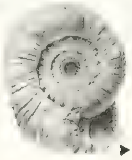

4b

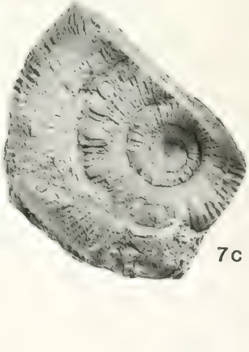

6a

6b


7a


7b


8


7c

EXPLANATION OF PLATE 12

All figures are natural size. The last suture is marked by an arrowhead.

Figure		Page
1.	*Reynesocoeloceras* cf. *incertum* (Fucini, 1905).	49
	1a,b. Specimen: GSC 98670 (latex cast); Locality: E51 (GSC Loc. C-117284); Fannin Formation, basal Kunae Zone.	
2,5,6.	*Reynesocoeloceras grahami,* new species.	49
	2a,b. Holotype: GSC 98671; Locality: FT1 (GSC Loc. C-177370); Rennell Junction Member, Freboldi Zone.	
	5. Paratype: GSC 98651; Locality: FT1 (GSC Loc. C-177370); Rennell Junction Member, Freboldi Zone.	
	6a,b. Paratype: GSC 87809; Locality: FT1 (GSC Loc. C-177370); Rennell Junction Member, Freboldi Zone.	
3,4,7,8.	*Reynesocoeloceras mortilleti* (Meneghini, 1875).	49
	3a,b. Hypotype: GSC 99032; Locality: FT2 (GSC Loc. C-177368); Fannin Formation, Kunae Zone.	
	4a,b. Hypotype: GSC 98673; Locality: DT1 (GSC Loc. O-48564); Fannin Formation, Kunae Zone.	
	7a-c. Hypotype: GSC 98675 (b = latex cast); Locality: DT1 (GSC Loc. O-48564); Fannin Formation, Kunae Zone.	
	8. Hypotype: GSC 98674; Locality: DT1 (GSC Loc. O-48564); Fannin Formation, Kunae Zone.	

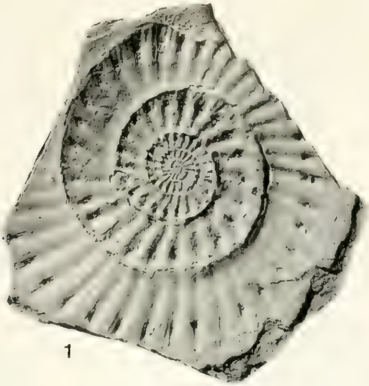
EXPLANATION OF PLATE 13

All figures are natural size.

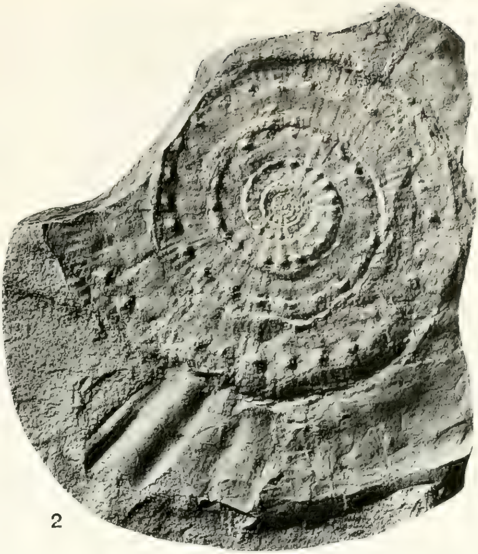
Figure — Page

1–4. *Pseudoskirroceras imlayi* Smith and Tipper, 1988. 41

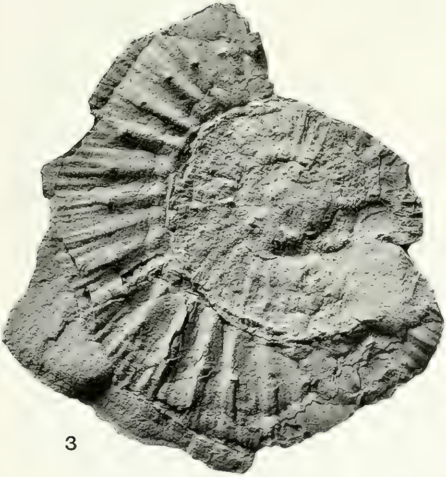
1. Holotype: GSC 87783 (latex cast); Locality: I08 (GSC Loc. C-90977); Ghost Creek Formation, Imlayi Zone.
2. Paratype: GSC 87785; Locality: I08 (GSC Loc. C-81733); Ghost Creek Formation, Imlayi Zone.
3. Hypotype: GSC 98678; Locality: I09 (GSC Loc. C-81707); Ghost Creek Formation, Imlayi Zone.
4. Paratype: GSC 87784; Locality: I08 (GSC Loc. C-81733); Ghost Creek Formation, Imlayi Zone.



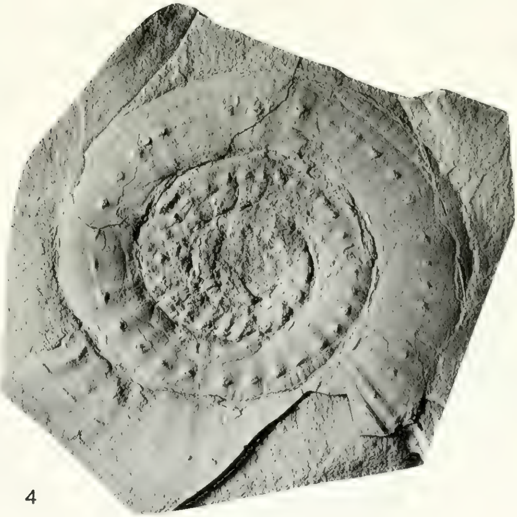
1



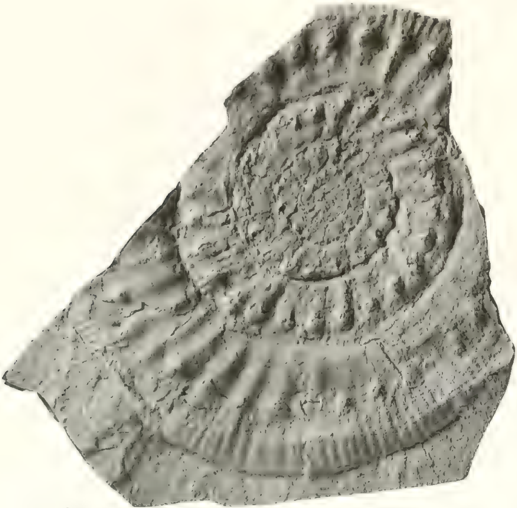
2

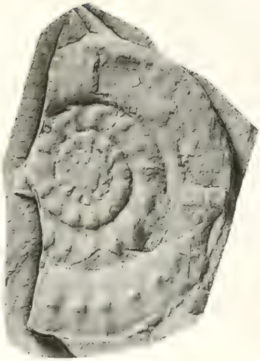


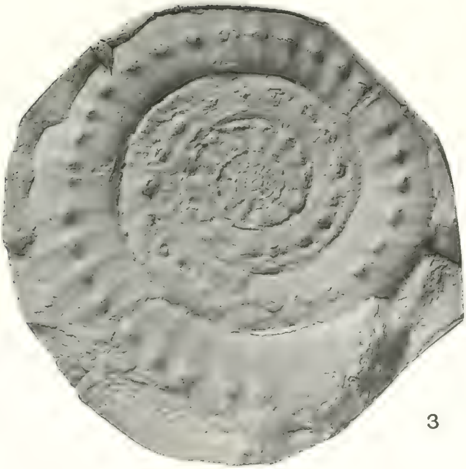
3

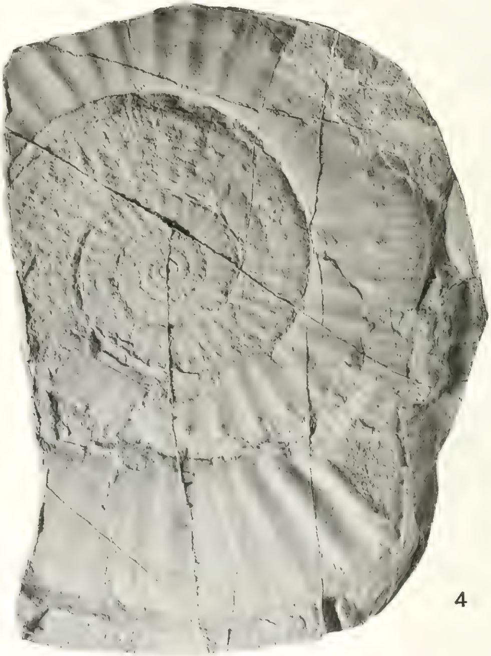


4


1


2


3


4

EXPLANATION OF PLATE 14

All figures are natural size.

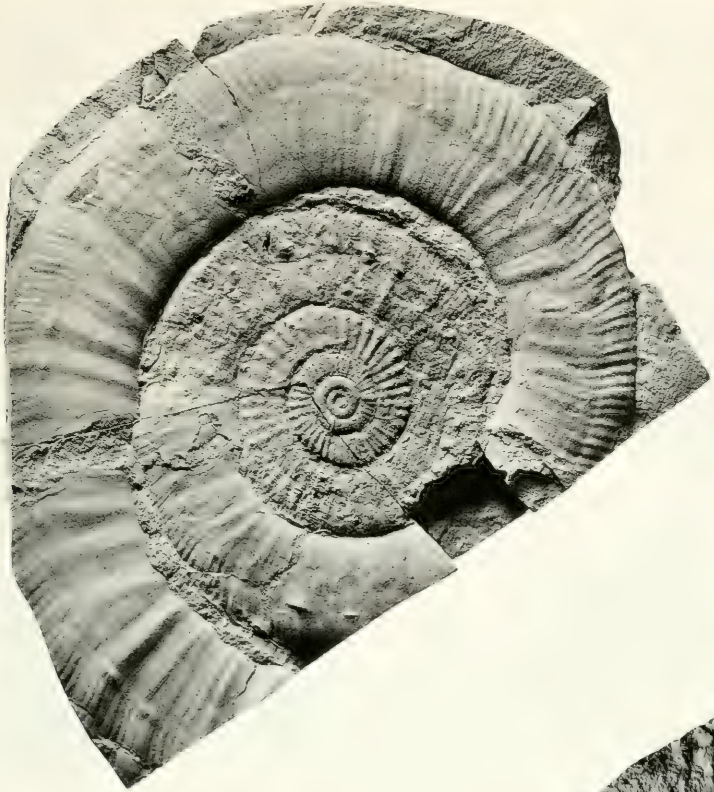
Figure		Page
1–4.	*Pseudoskirroceras imlayi* Smith and Tipper, 1988.	41

1. Hypotype: GSC 95572; Locality: I08 (GSC Loc. C-157551); Ghost Creek Formation, Imlayi Zone.
2. Hypotype: GSC 98737; Locality: I08 (GSC Loc. C-157551); Ghost Creek Formation, Imlayi Zone.
3. Hypotype: GSC 98700 (latex cast); Locality: I08 (GSC Loc. C-157551); Ghost Creek Formation, Imlayi Zone.
4. Hypotype: GSC 98715 (latex cast); Locality: I08 (GSC Loc. C-157551); Ghost Creek Formation, Imlayi Zone.

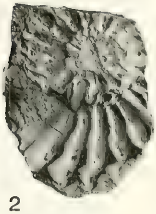
EXPLANATION OF PLATE 15

All figures are natural size.

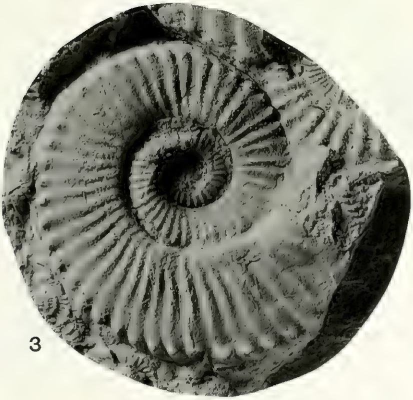
Figure		Page
1.	*Pseudoskirroceras imlayi* Smith and Tipper, 1988.	41
	Hypotype: GSC 98680; Locality: I08 (GSC Loc. C-90977); Ghost Creek Formation, Imlayi Zone.	
2.	*Phricodoceras* cf. *taylori* (J. de C. Sowerby, 1826).	41
	Specimen: GSC 87789 (latex cast); Locality: I08 (GSC Loc. C-90974); Ghost Creek Formation, Imlayi Zone.	
3,4.	*Dubariceras silviesi* (Hertlein, 1925).	43
	3. Hypotype: GSC 87792; Locality: GT3 (GSC Loc. C-81712); Rennell Junction Member.	
	4. Hypotype: GSC 98683; Locality: I02 (GSC Loc. O-93721); Rennell Junction Member, Whiteavesi Zone.	



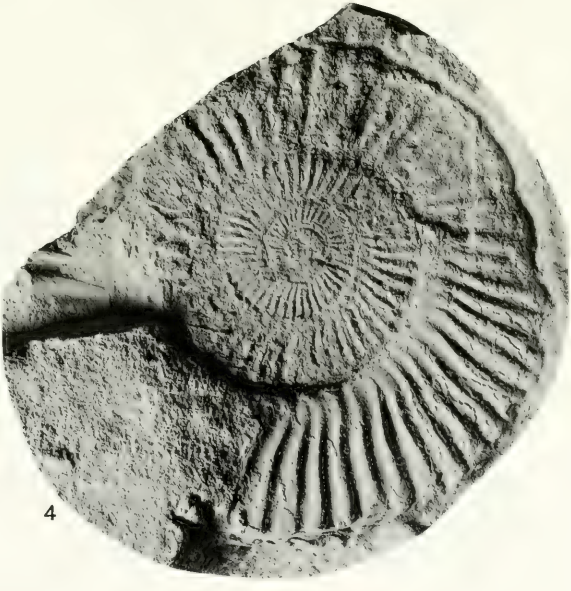
1



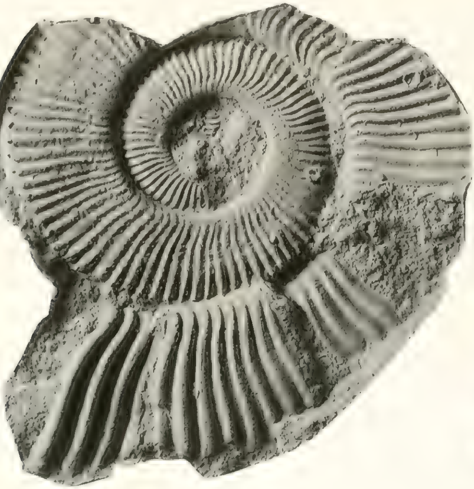
2

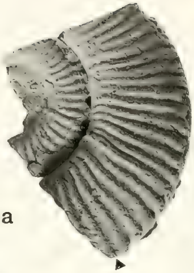


3

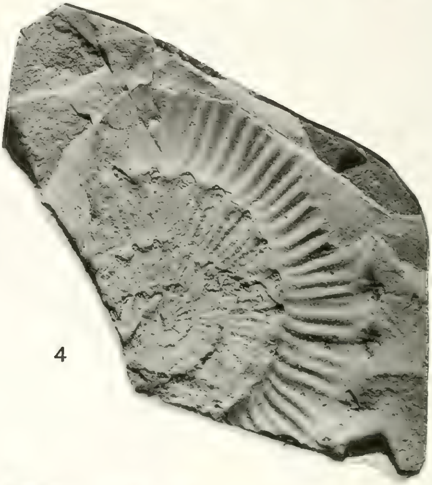


4

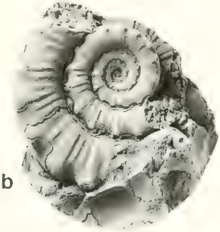

1


2a

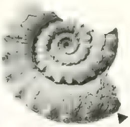
2b

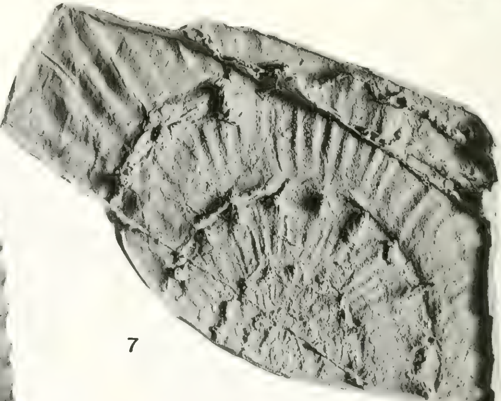

4

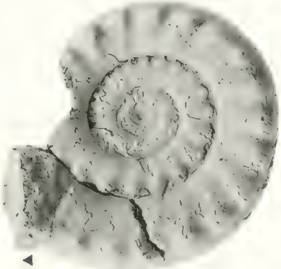
3a


3b

5a


5b


7


6a

6b

EXPLANATION OF PLATE 16

All figures are natural size. The last suture is marked by an arrowhead.

Figure Page

1,2. *Dubariceras freboldi* Dommergues, Mouterde, and Rivas, 1984. 42
  1. Hypotype: GSC 87794 (latex cast); Locality: GT3 (GSC Loc. C-90587); Rennell Junction Member, Freboldi Zone.
  2a,b. Hypotype: GSC 98686; Locality: E48 (GSC Loc. C-90554); Rennell Junction Member, Freboldi Zone.

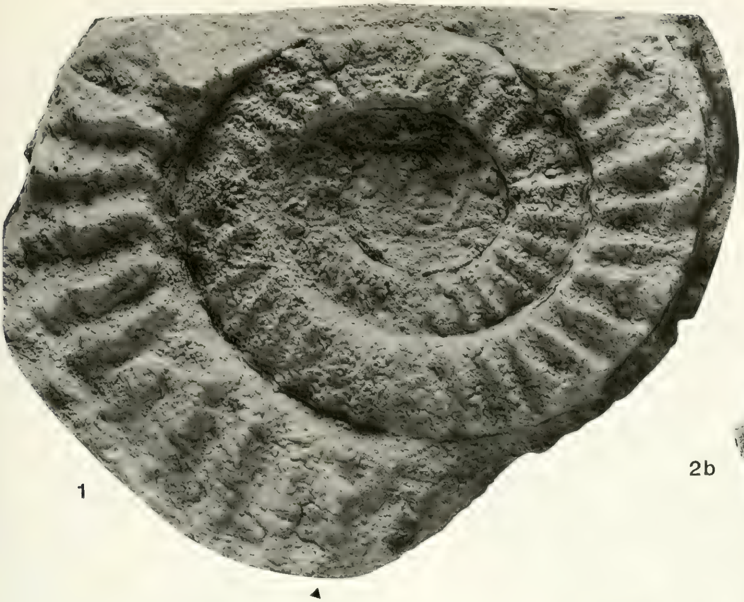
3–5,7. *Metaderoceras evolutum* (Fucini, 1921). 44
  3a,b. Hypotype: GSC 95576; Locality: E27 (GSC Loc. O-91794); Rennell Junction Member, Whiteavesi Zone.
  4. Hypotype: GSC 98688 (latex cast); Locality: D03 (GSC Loc. O-93565); Ghost Creek Formation, Whiteavesi Zone.
  5a,b. Hypotype: GSC 98689; Locality: ET1 (GSC Loc. O-48603).
  7. Hypotype: GSC 98691 (latex cast); Locality: D03 (GSC Loc. O-93565); Ghost Creek Formation, Whiteavesi Zone.

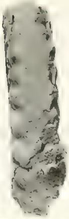
6. *Metaderoceras*? aff. *mouterdei* (Frebold, 1970). 45
  6a,b. Specimen: GSC 87797; Locality: C03 (GSC Loc. C-80610); Fannin Formation, Freboldi Zone.

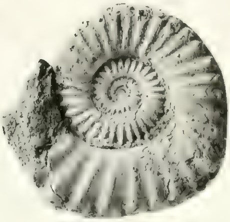
EXPLANATION OF PLATE 17

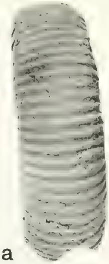
All figures are natural size. The last suture is marked by an arrowhead.

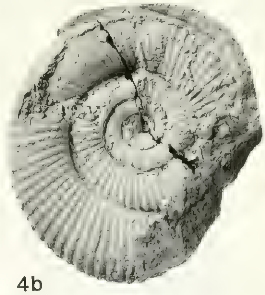
Figure		Page
1.	*Metaderoceras* sp.	46
	Specimen: GSC 98702; Locality: BT1 (GSC Loc. C-117025); Ghost Creek Formation, Imlayi Zone.	
2,3.	*Metaderoceras talkeetnaense* Thomson and Smith, 1992.	45
	2a,b. Hypotype: GSC 98703; Locality: E38 (GSC Loc. C-80348); Rennell Junction Member, Whiteavesi Zone.	
	3. Hypotype: GSC 98704; Locality: GT1 (GSC Loc. C-90579); Rennell Junction Member, Whiteavesi Zone.	
4,5.	*Reynesoceras colubriforme* (Bettoni, 1900).	46
	4a,b. Hypotype: GSC 87796; Locality: E57 (GSC Loc. C-90614); Fannin Formation, Kunae Zone.	
	5a,b. Hypotype: GSC 98706; Locality: E57 (GSC Loc. C-90614); Fannin Formation, Kunae Zone.	

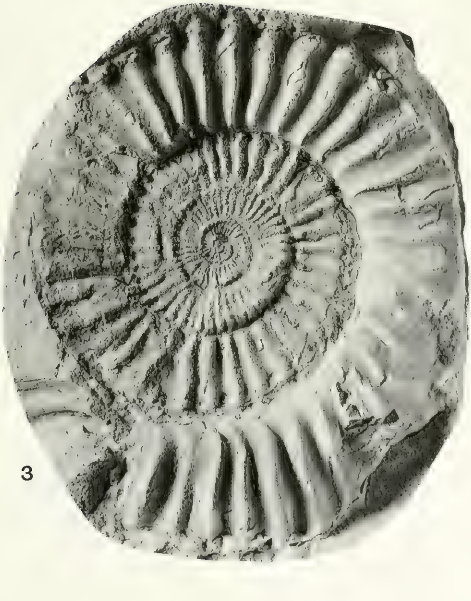

1

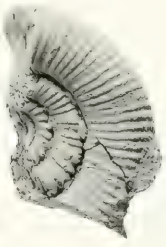

2a

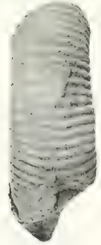

2b

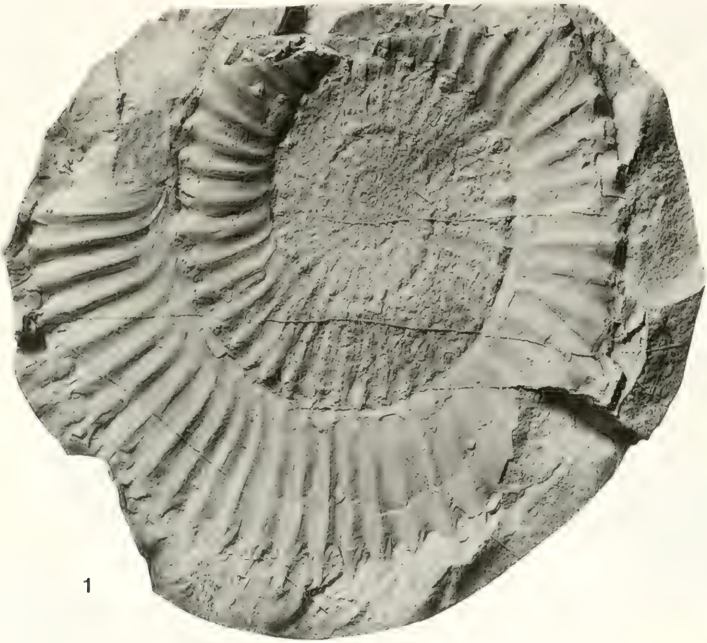

4a

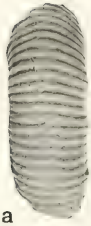

4b

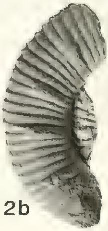

3

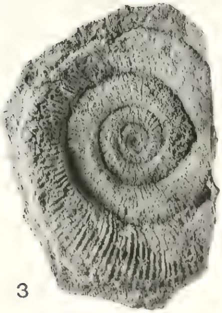

5a

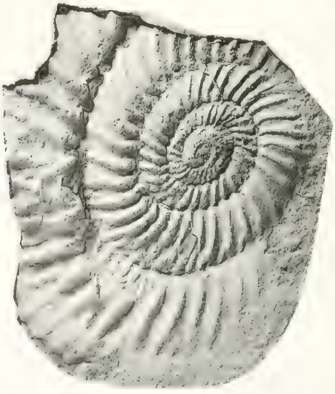

5b

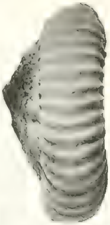

1

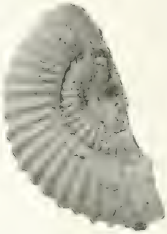

2a


2b

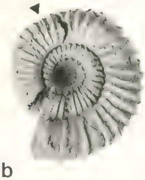

3

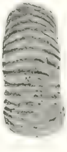

4

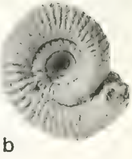

5a


5b

6a


6b


7a


7b

EXPLANATION OF PLATE 18

All figures are natural size. The last suture is marked by an arrowhead.

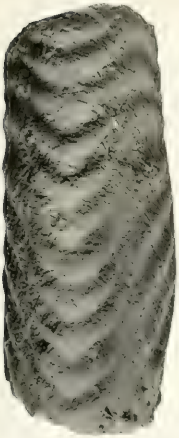
Figure		Page
1.	*Metaderoceras evolutum* (Fucini, 1921). Hypotype: GSC 98707 (latex cast); Locality: D07 (GSC Loc. C-80249); Ghost Creek Formation, Whiteavesi Zone.	44
2.	*Reynesoceras* aff. *colubriforme* (Bettoni, 1900). 2a,b. Specimen: GSC 98708; Locality: E57 (GSC Loc. C-90614); Fannin Formation, Kunae Zone.	46
3.	*Reynesoceras italicum* (Fucini, 1901). Hypotype: GSC 98712 (latex cast); Locality: I05 (GSC Loc. O-93723); Fannin Formation, Kunae Zone.	47
4.	*Reynesoceras*? sp. Specimen: GSC 98709 (latex cast); Locality: ET4 (GSC Loc. O-93579); Fannin Formation, Kunae Zone.	48
5.	*Reynesoceras* sp. 5a,b. Specimen: GSC 98672; Locality: E57 (GSC Loc. C-90614); Fannin Formation, Kunae Zone.	48
6,7.	*Reynesoceras ragazzonii* (Hauer, 1861). 6a,b. Hypotype: GSC 87800; Locality: DT1 (GSC Loc. O-48564); Fannin Formation, Kunae Zone. 7a,b. Hypotype: GSC 98714; Locality: I06 (GSC Loc. C-90542); Fannin Formation, Kunae Zone.	47

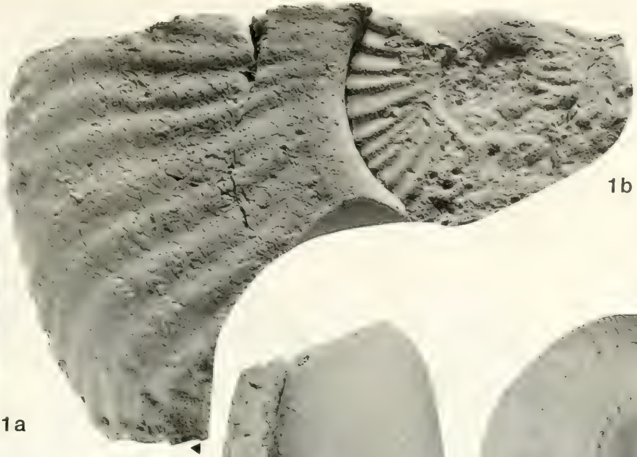
EXPLANATION OF PLATE 19

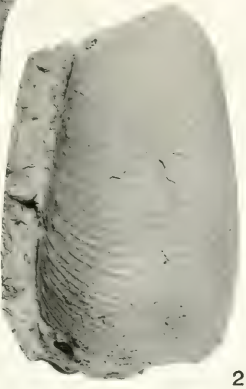
All figures are natural size. The last suture is marked by an arrowhead.

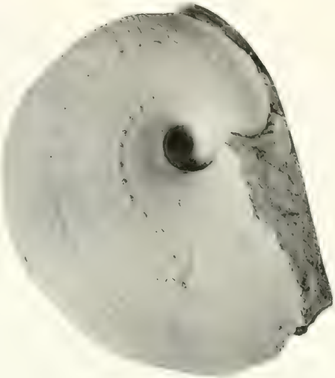
Figure Page

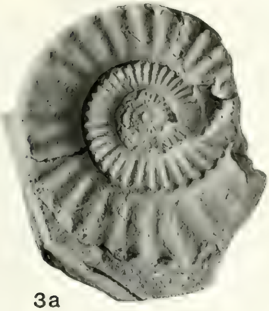
1. *Amaltheus stokesi* (J. Sowerby, 1818). 51
   1a,b. Hypotype: GSC 98711; Locality: FT2 (GSC Loc. C-56954); Fannin Formation, Kunae Zone.
2. *Liparoceras* (*Becheiceras*) *bechei* (J. de C. Sowerby, 1821). 52
   2a,b. Hypotype: GSC 99033; Locality: FT2 (GSC Loc. C-177368); Fannin Formation, Kunae Zone.
3. *Metaderoceras mouterdei* (Frebold, 1970). 44
   3a,b. Holotype: GSC 20337; Locality: ET1 (GSC Loc. O-48603).
4. *Metaderoceras*? aff. *mouterdei* (Frebold, 1970). 45
   4a,b. Specimen: GSC 98692; Locality: C03 (GSC Loc. C-117027); Fannin Formation, Freboldi Zone.

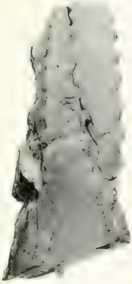

1a

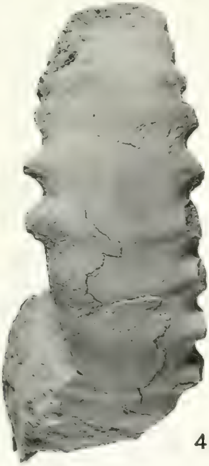

1b

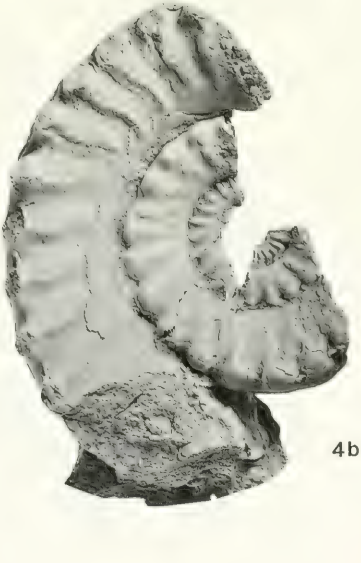

2a

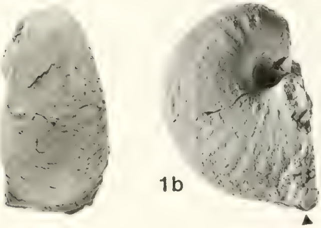

2b

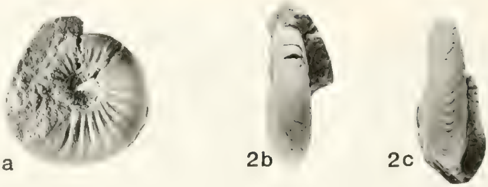

3a

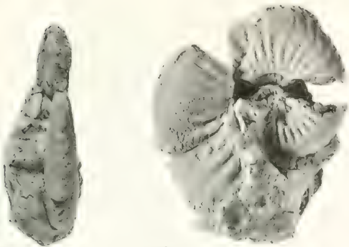

3b

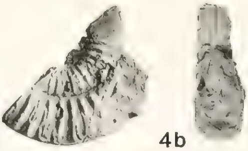

4a

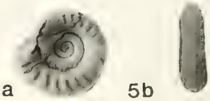

4b

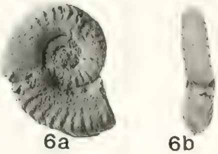

1a 1b

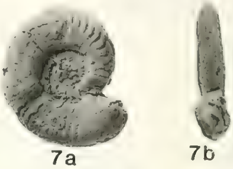

2a 2b 2c

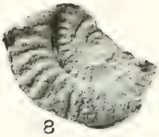

3a 3b

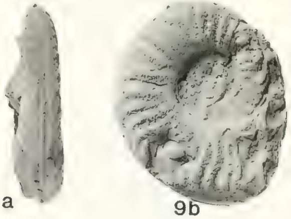

4a 4b

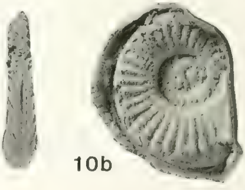

5a 5b

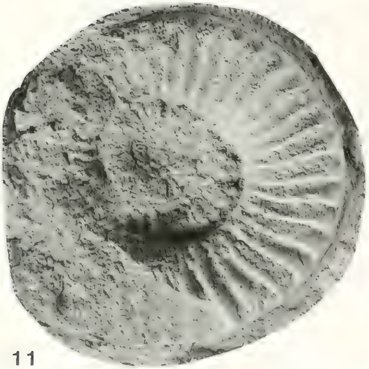

6a 6b

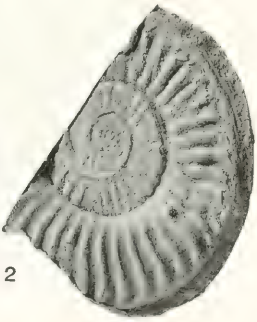

7a 7b

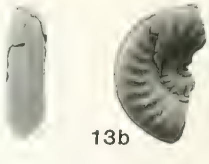

8

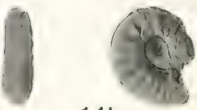

9a 9b


10a 10b


11


12


13a 13b


14a 14b

EXPLANATION OF PLATE 20

All figures are natural size. The last suture is marked by an arrowhead.

Figure		Page
1.	*Liparoceras* (*Becheiceras*) *bechei* (J. Sowerby, 1821).	52
	1a,b. Hypotype: GSC 78715; Locality: E32 (GSC Loc. O-91807); Rennell Junction Member, Whiteavesi Zone.	
2.	*Amaltheus viligaensis* (Tuchkov, 1954).	51
	2a-c. Hypotype: GSC 87805; Locality: E62 (GSC Loc. C-81716); Fannin Formation, Carlottense Zone.	
3.	*Amaltheus stokesi* (J. Sowerby, 1818).	51
	3a,b. Hypotype: GSC 98717; Locality: GT4 (GSC Loc. C-81927); Fannin Formation, Kunae Zone.	
4.	*Arieticeras* aff. *domarense* (Meneghini, 1867).	55
	4a,b. Specimen: GSC 98718; Locality: ET5 (GSC Loc. C-117002); Fannin Formation, Carlottense Zone.	
5.	*Arieticeras disputabile* (Fucini, 1908).	54
	5a,b. Hypotype: GSC 98719; Locality: GT4 (GSC Loc. C-81927); Fannin Formation, Kunae Zone.	
6,7.	*Arieticeras lupheri* Imlay, 1968.	55
	6a,b. Hypotype: GSC 98720; Locality: I06 (GSC Loc. C-90542); Fannin Formation, Kunae Zone. 7a,b. Hypotype: GSC 98721; Locality: I06 (GSC Loc. C-90542); Fannin Formation, Kunae Zone.	
8.	*Arieticeras* cf. *micrasterias* (Meneghini, 1874).	56
	Specimen: GSC 98722 (latex cast); Locality: I17 (GSC Loc. C-81703); Fannin Formation, Kunae Zone.	
9,10.	*Arieticeras* cf. *ruthenense* (Reynès, 1868).	56
	9a,b. Specimen: GSC 98723; Locality: I06 (GSC Loc. C-90542); Fannin Formation, Kunae Zone. 10a,b. Specimen: GSC 98724 (b = latex cast); Locality: I14 (GSC Loc. C-81730); Fannin Formation, Kunae Zone.	
11,12.	*Arieticeras* aff. *algovianum* (Oppel, 1862).	54
	11. Specimen: GSC 98725; Locality: I17 (GSC Loc. C-81703); Fannin Formation, Kunae Zone. 12. Specimen: GSC 98726 (latex cast); Locality: I17 (GSC Loc. C-81703); Fannin Formation, Kunae Zone.	
13.	*Oregonites*? *dawsoni*, new species.	59
	Holotype: GSC 98727; Locality: E63 (GSC Loc. O-93750); Fannin Formation, Carlottense Zone.	
14.	*Fieldingiceras fieldingii* (Reynès, 1868).	60
	14a,b. Hypotype: GSC 98728; Locality: ET5 (GSC Loc. C-117031); Fannin Formation, Carlottense Zone.	

EXPLANATION OF PLATE 21

All figures are natural size. The last suture is marked by an arrowhead.

Figure — Page

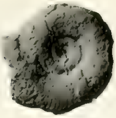
1,4. *Fieldingiceras pseudofieldingii* (Fucini, 1904) 60
   1a,b. Hypotype: GSC 99025; Locality: I07 (GSC Loc. C-177355); Fannin Formation, Kunae Zone.
   4a,b. Hypotype: GSC 99036; Locality: FT2 (GSC Loc. C-177368); Fannin Formation, Kunae Zone.

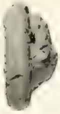
2. *Arieticeras disputabile* (Fucini, 1908) 54
   2a,b. Hypotype: GSC 99037; Locality: FT2 (GSC Loc. C-177368); Fannin Formation, Kunae Zone.

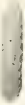
3. *Fieldingiceras fieldingii* (Reynès, 1868) 60
   3a,b. Hypotype: GSC 99040; Locality: ET5 (GSC Loc. C-80833); Fannin Formation, Carlottense Zone.

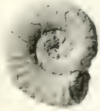
5. *Canavaria*? sp. 59
   Specimen: GSC 98698; Locality: E61 (GSC Loc. C-80825); Fannin Formation, Carlottense Zone.

6,7. *Fuciniceras* sp. 63
   6a,b. Specimen: GSC 99035; Locality: FT2 (GSC Loc. C-177368); Fannin Formation, Kunae Zone.
   7a,b. Specimen: GSC 99034; Locality: FT2 (GSC Loc. C-177368); Fannin Formation, Kunae Zone.

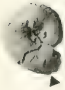

1a

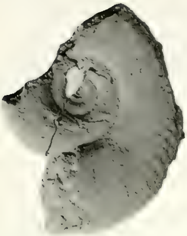

1b

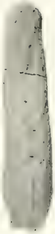

2a

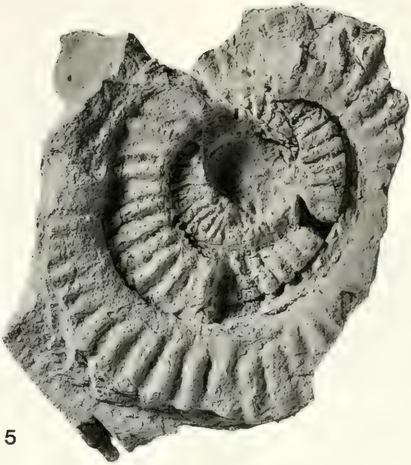

2b

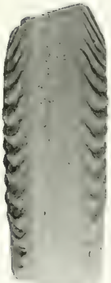
3a

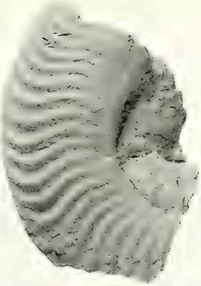

3b

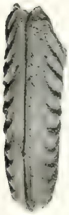

4a

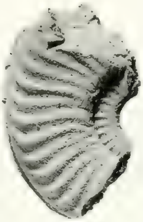

4b

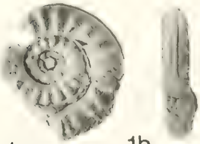

5

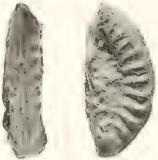

6a

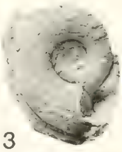

6b

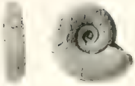

7a

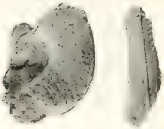

7b

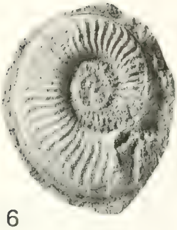

1a 1b

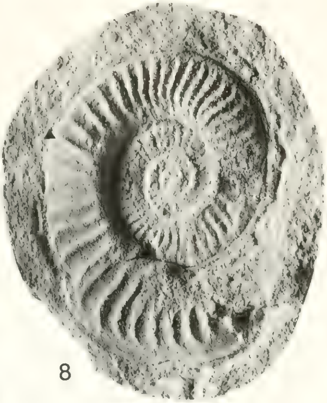

2a 2b

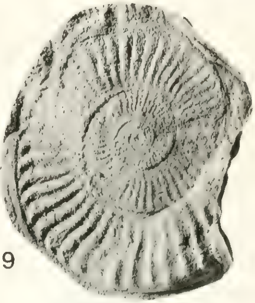

3

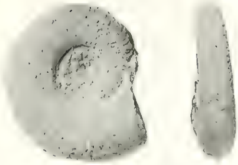

4a 4b

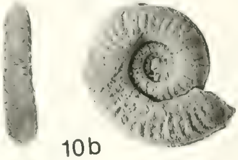

5a 5b

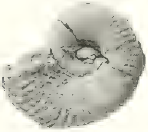

6

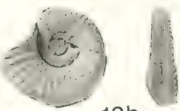

8

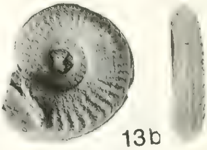

9

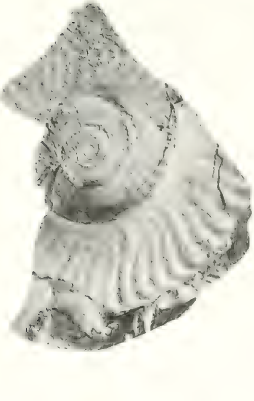

7a 7b

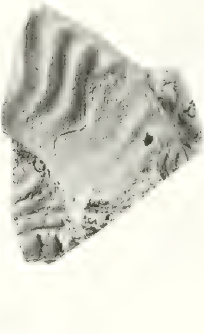

10a 10b

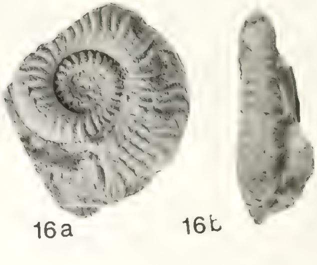

11


12a 12b


13a 13b


14


15a


16a 16b

EXPLANATION OF PLATE 22

All figures are natural size.

Figure		Page
1,2.	*Fontanelliceras* sp.	58
	1a,b. Specimen: GSC 98583; Locality: E52 (GSC Loc. C-90553); Fannin Formation, Kunae Zone.	
	2a,b. Specimen: GSC 98584; Locality: D22 (GSC Loc. C-80768); Fannin Formation, Kunae Zone.	
3–5.	*Fieldingiceras pseudofieldingii* (Fucini, 1904).	60
	3. Hypotype: GSC 98587; Locality: I06 (GSC Loc. C-90542); Fannin Formation, Kunae Zone.	
	4a,b. Hypotype: GSC 98590; Locality: D20 (GSC Loc. C-80765); Fannin Formation, Kunae Zone.	
	5a,b. Hypotype: GSC 98591; Locality: I06 (GSC Loc. C-90542); Fannin Formation, Kunae Zone.	
6,8–9.	*Leptaleoceras* aff. *accuratum* (Fucini, 1931).	57
	6. Specimen: GSC 95577 (latex cast); Locality: I17 (GSC Loc. C-81703); Fannin Formation, Kunae Zone.	
	8. Specimen: GSC 98593; Locality: I17 (GSC Loc. C-81703); Fannin Formation, Kunae Zone.	
	9. Specimen: GSC 98599 (latex cast); Locality: I17 (GSC Loc. C-81703); Fannin Formation, Kunae Zone.	
10.	*Leptaleoceras compressum* (Monestier, 1934).	57
	10a,b. Hypotype: GSC 98601; Locality: I06 (GSC Loc. C-90542); Fannin Formation, Kunae Zone.	
7,11–13.	*Leptaleoceras* sp.	58
	7a,b. Specimen: GSC 98592; Locality: FT2 (GSC Loc. C-177368); Fannin Formation, Kunae Zone.	
	11. Specimen: GSC 98605; Locality: I06 (GSC Loc. C-90542); Fannin Formation, Kunae Zone.	
	12a,b. Specimen: GSC 98602; Locality: I06 (GSC Loc. C-90542); Fannin Formation, Kunae Zone.	
	13a,b. Specimen: GSC 98604; Locality: I06 (GSC Loc. C-90542); Fannin Formation, Kunae Zone.	
14,15.	*Fuciniceras* cf. *targionii* Fucini, 1905.	61
	14. Specimen: GSC 98606; Locality: I17 (GSC Loc. C-81703); Fannin Formation, Kunae Zone.	
	15. Specimen: GSC 98609; Locality: I17 (GSC Loc. C-81703); Fannin Formation, Kunae Zone.	
16.	*Fuciniceras* aff. *intumescens* (Fucini, 1901).	63
	16a,b. Specimen: GSC 87801; Locality: E52 (GSC Loc. C-90553); Fannin Formation, Kunae Zone.	

EXPLANATION OF PLATE 23

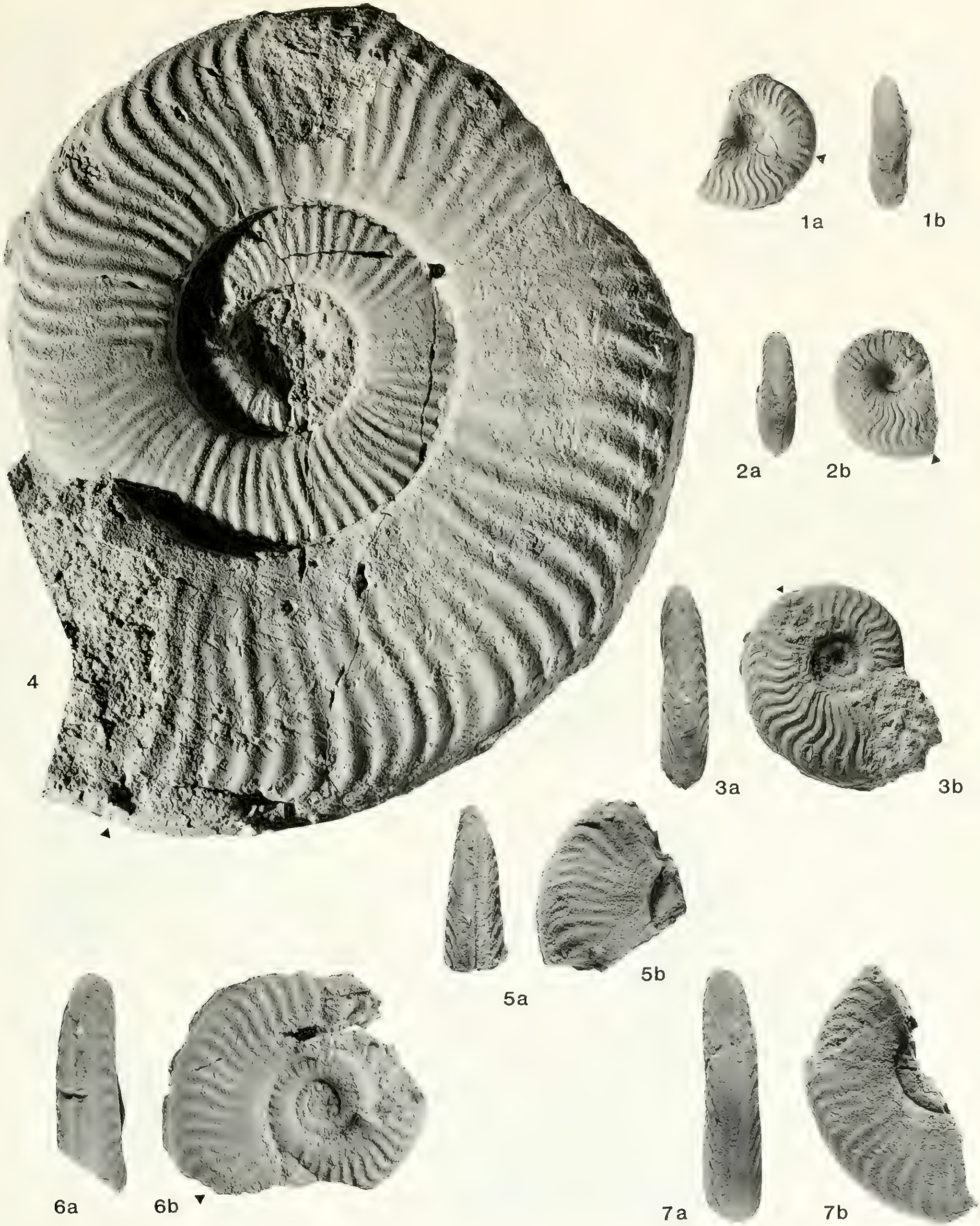
All figures are natural size. The last suture is marked by an arrowhead.

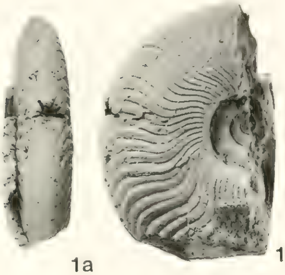
Figure — Page

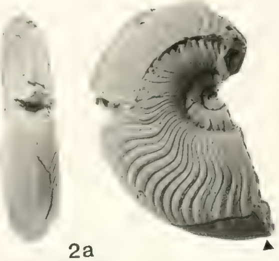
1–3. *Protogrammoceras* (*Protogrammoceras*)? sp. 64
    1a,b. Specimen: GSC 98744; Locality: ET5 (GSC Loc. C-80834); Fannin Formation, Carlottense Zone.
    2a,b. Specimen: GSC 98745; Locality: E63 (GSC Loc. O-93750); Fannin Formation, Carlottense Zone.
    3a,b. Specimen: GSC 99016; Locality: E62 (GSC Loc. C-81716); Fannin Formation, Carlottense Zone.

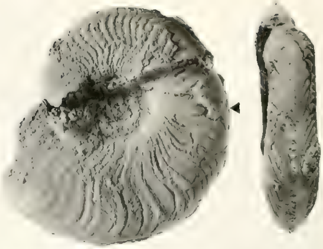
4. Genus and species indet. 67
    Specimen: GSC 99013; Locality: FT2 (GSC Loc. C-56954); Fannin Formation, Kunae Zone.

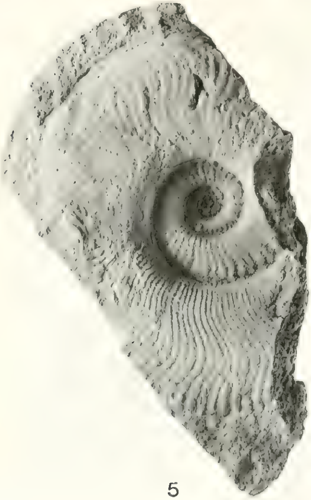
5–7. *Protogrammoceras* (*Matteiceras*) cf. *diornatum* Dommergues, Meister and Fauré, 1985. 67
    5a,b. Specimen: GSC 98743; Locality: I06 (GSC Loc. C-90542); Fannin Formation, Kunae Zone.
    6a,b. Specimen: GSC 99014; Locality: FT2 (GSC Loc. C-56954); Fannin Formation, Kunae Zone.
    7a,b. Specimen: GSC 98742; Locality: D20 (GSC Loc. C-80765); Fannin Formation, Kunae Zone.

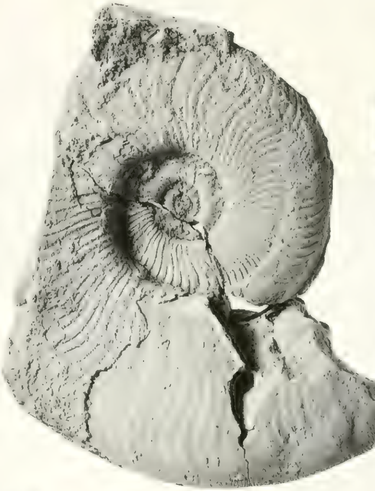

1a
1b
2a
2b
4
3a
3b
5a
5b
6a
6b
7a
7b

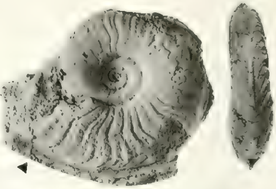

1a 1b

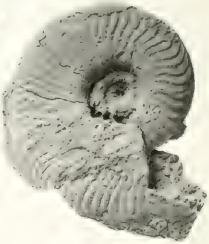

2a 2b

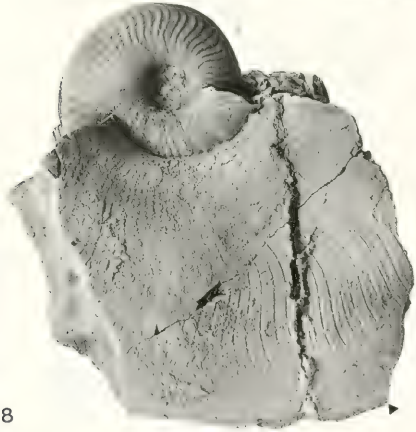

3a 3b

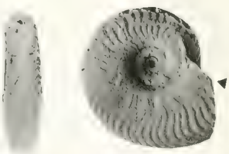

5


6


4a 4b


7


8


9a 9b

EXPLANATION OF PLATE 24

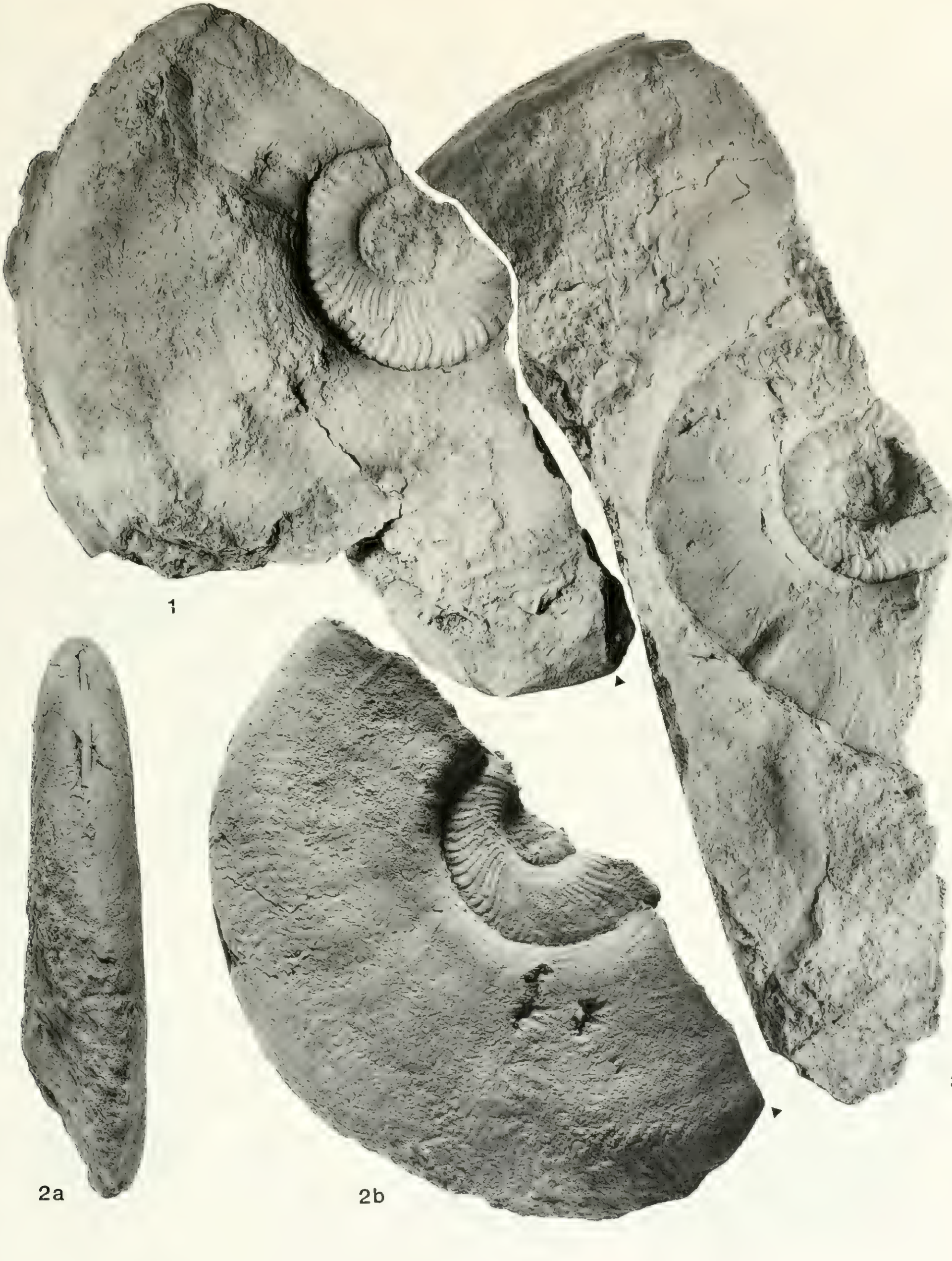
All figures are natural size. The last suture is marked by an arrowhead.

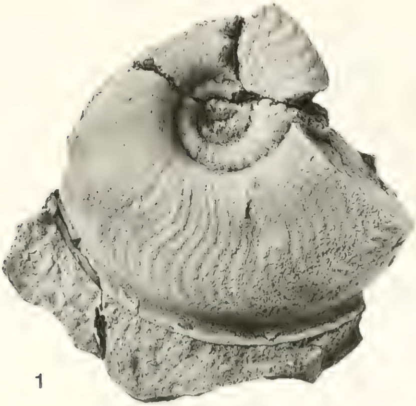
Figure	Page
1–4. *Protogrammoceras* (*Protogrammoceras*) cf. *paltum* (Buckman, 1922).	66
1a,b. Specimen: GSC 98747; Locality: I03 (GSC Loc. C-90559); Fannin Formation, Carlottense Zone.	
2a,b. Specimen: GSC 99015; Locality: ET5 (GSC Loc. C-117005); Fannin Formation, Carlottense Zone.	
3a,b. Specimen: GSC 98697; Locality: ET5 (GSC Loc. C-117003); Fannin Formation, Carlottense Zone.	
4a,b. Specimen: GSC 98746; Locality: D27 (GSC Loc. C-80776); Fannin Formation, Lower Toarcian.	
5,6. *Protogrammoceras* (*Protogrammoceras*) *kurrianum* (Oppel, 1862).	64
5. Hypotype: GSC 98733; Locality: D24 (GSC Loc. O-93754); Fannin Formation, Carlottense Zone.	
6. Hypotype: GSC 87808; Locality: E68 (GSC Loc. C-80786); Fannin Formation, Carlottense Zone.	
7–9. *Protogrammoceras* (*Protogrammoceras*) *aequiondulatum* (Bettoni, 1900).	63
7. Hypotype: GSC 98734; Locality: ET5 (GSC Loc. C-117031); Fannin Formation, Carlottense Zone.	
8. Hypotype: GSC 98649; Locality: E63 (GSC Loc. C-90545); Fannin Formation, Carlottense Zone.	
9a,b. Hypotype: GSC 98735; Locality: ET5 (GSC Loc. C-117031); Fannin Formation, Carlottense Zone.	

EXPLANATION OF PLATE 25

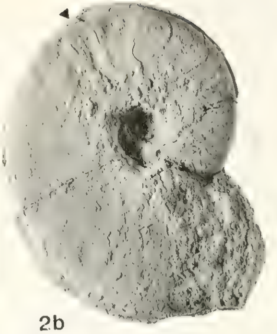
All figures are natural size. The last suture is marked by an arrowhead.

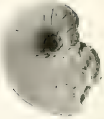
Figure		Page
1–3.	*Protogrammoceras* (*Protogrammoceras*) *skidegatense*, new species.	66
1.	Paratype: GSC 98741; Locality: E63 (GSC Loc. C-90545); Fannin Formation, Carlottense Zone.	
2a,b.	Holotype: GSC 98740; Locality: D25 (GSC Loc. C-80772); Fannin Formation, Carlottense Zone.	
3.	Paratype: GSC 98739; Locality: D24 (GSC Loc. C-0–93574); Fannin Formation, Carlottense Zone.	


1
2a
2b
3

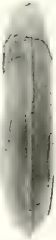

1

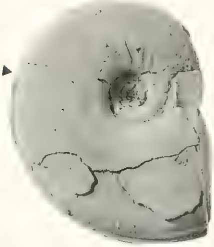
2a

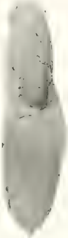

2b


3a

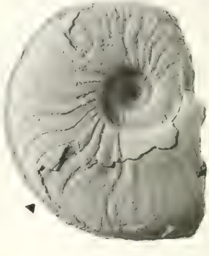
3b

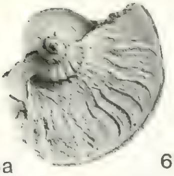

4a


4b

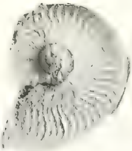

4c

5a


5b

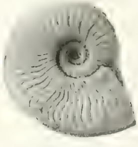

6a

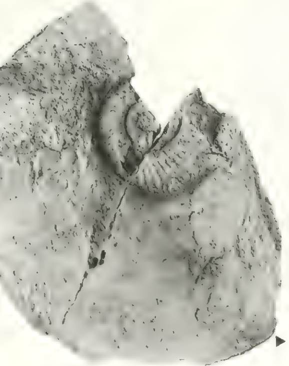
6b

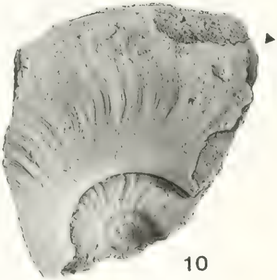

7a

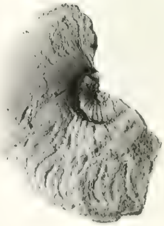
7b

8a


8b


9


10


11

EXPLANATION OF PLATE 26

All figures are natural size. The last suture is marked by an arrowhead.

Figure		Page
1.	*Lioceratoides (Lioceratoides) maurelli* (McLearn, 1930).	69
	Holotype: GSC 9052; Locality: DT2 (GSC Loc. O-13630); Fannin Formation, Carlottense Zone or Lower Toarcian.	
2–4.	*Lioceratoides* (*Lioceratoides*) *involutum*, new species.	69
	2a,b. Paratype: GSC 98644; Locality: ET5 (GSC Loc. C-81917); Fannin Formation, Carlottense Zone.	
	3a,b. Paratype: GSC 98705; Locality: E62 (GSC Loc. C-81716); Fannin Formation, Carlottense Zone.	
	4a-c. Holotype: GSC 98716; Locality: ET5 (GSC Loc. 0–48563; Fannin Formation, Carlottense Zone.	
5,6,9–11.	*Lioceratoides* (*Lioceratoides*) *allifordense* (McLearn, 1930).	68
	5a,b. Hypotype: GSC 98641; Locality: E67 (GSC Loc. C-807853); Fannin Formation, Carlottense Zone.	
	6a,b. Hypotype: GSC 98643; Locality: D24 (GSC Loc. O-93574); Fannin Formation, Carlottense Zone	
	9. Holotype: GSC 9053; Locality: DT2 (GSC Loc. C-117033); Fannin Formation, Carlottense Zone or Lower Toarcian.	
	10. Hypotype: GSC 98736; Locality: E65 (GSC Loc. O-91835); Fannin Formation, Carlottense Zone.	
	11. Hypotype: GSC 99046; Locality: DT2 (GSC Loc. O-13630); Formation, Zone.	
7,8.	*Lioceratoides* (*Lioceratoides*) sp. juv.	69
	7a,b. Specimen: GSC 6489 (*Harpoceras* sp. A of McLearn, 1932); Locality: DT2 (GSC Loc. C-117033); Fannin Formation, Carlottense Zone or Lower Toarcian.	
	8a,b. Specimen: GSC 98642; Locality: D26 (GSC Loc. O-93582); Fannin Formation, Lower Toarcian.	

EXPLANATION OF PLATE 27

All figures are natural size. The last suture is marked by an arrowhead.

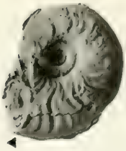
Figure Page

1,2. *Lioceratoides* (*Lioceratoides*) cf. *grecoi* (Fucini, 1901). 68

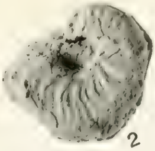
1a,b. Specimen: GSC 98677; Locality: ET5 (GSC Loc. C-117002); Fannin Formation, Carlottense Zone.
2. Specimen: GSC 98679; Locality: E62 (GSC Loc. C-81716); Fannin Formation, Carlottense Zone.

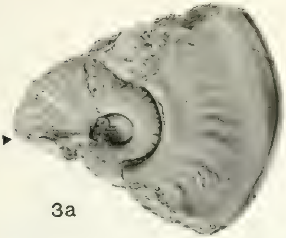
3–7. *Lioceratoides* (*Pacificeras*) *angionus* (Fucini, 1931). 71

3a,b. Hypotype: GSC 98611; Locality: E65 (GSC Loc. C-80783); Fannin Formation, Carlottense Zone.
4. Hypotype: GSC 99045; Locality: ET5 (GSC Loc. C-117003); Fannin Formation, Carlottense Zone.
5a,b. Hypotype: GSC 98634; Locality: E67 (GSC Loc. C-80785); Fannin Formation, Carlottense Zone.
6a,b. Hypotype: GSC 98640; Locality: E65 (GSC Loc. O-91835); Fannin Formation, Carlottense Zone.
7a-c. Hypotype: GSC 98732; Locality: D24 (GSC Loc. O-93574); Fannin Formation, Carlottense Zone.

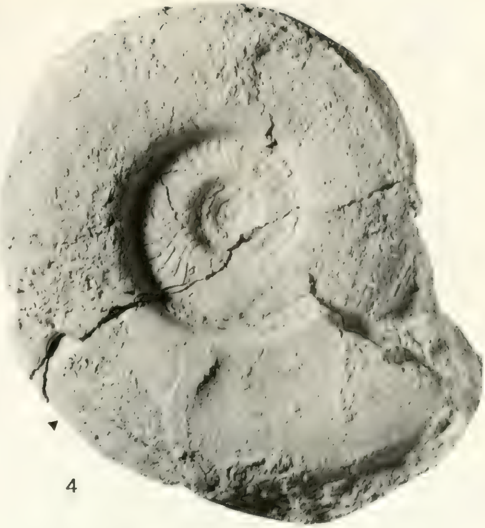

1a

1b

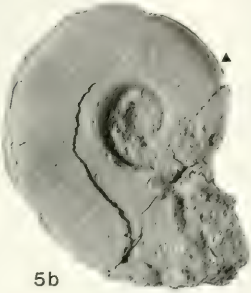

2

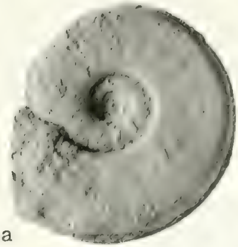

3a

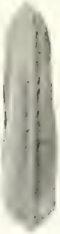
3b


4

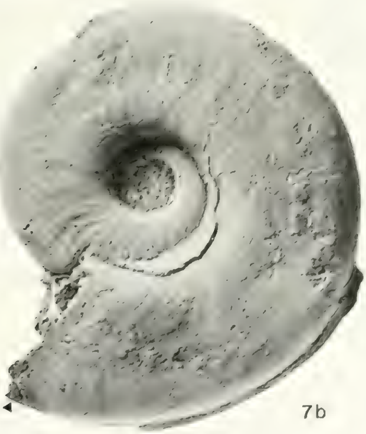
5a


5b

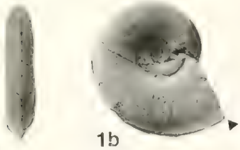

6a

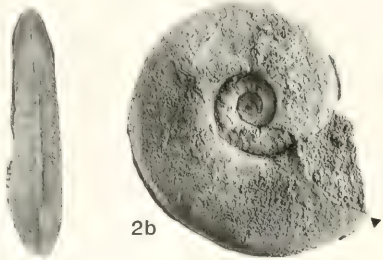

6b

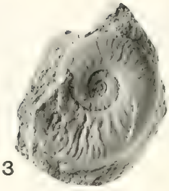
7a

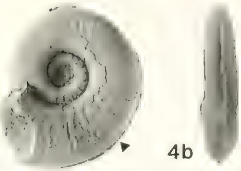

7b

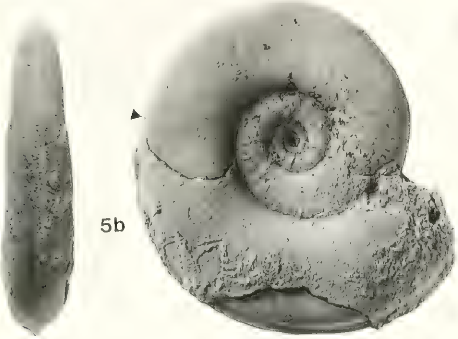
7c

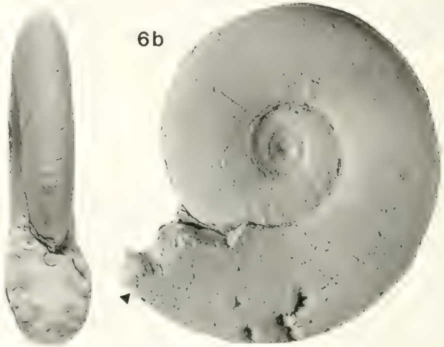

1a 1b

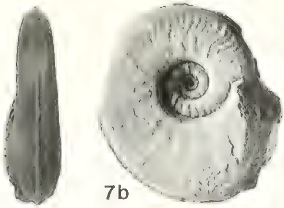

2a 2b

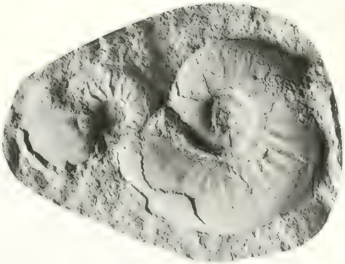

3

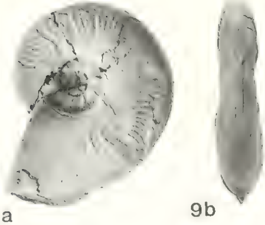

4a 4b

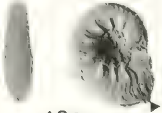

5a 5b

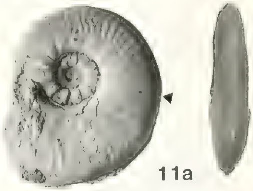

6a 6b


7a 7b


8


9a 9b


10a 10b


11a 11b

EXPLANATION OF PLATE 28

All figures are natural size. The last suture is marked by an arrowhead.

Figure Page

1–11. *Lioceratoides* (*Pacificeras*) *propinquum* (Whiteaves, 1884). 71

1a,b. Hypotype: GSC 98681; Locality: E63 (GSC Loc. C-90545); Fannin Formation, Carlottense Zone.

2a,b. Lectotype: GSC 4877; Locality: DT2 (GSC Loc. C-117033); Fannin Formation, Carlottense Zone or Lower Toarcian.

3. Hypotype: GSC 98682; Locality: E63 (GSC Loc. C-90545); Fannin Formation, Carlottense Zone.

4a,b. Hypotype: GSC 98685; Locality: ET5 (GSC Loc. C-80824); Fannin Formation, Carlottense Zone.

5a,b. Hypotype: GSC 87804; Locality: ET5 (GSC Loc. C-117003); Fannin Formation, Carlottense Zone.

6a,b. Hypotype: GSC 98687; Locality: E62 (GSC Loc. C-81716); Fannin Formation, Carlottense Zone.

7a,b. Plesiotype of McLearn (1932): GSC 6491; Locality: DT2 (GSC Loc. C-117033); Fannin Formation, Carlottense Zone or Lower Toarcian.

8. Hypotype: GSC 98661 (latex cast); Locality: E67 (GSC Loc. C-80785); Fannin Formation, Carlottense Zone.

9a,b. Hypotype: GSC 98655; Locality: E67 (GSC Loc. C-80785); Fannin Formation, Carlottense Zone.

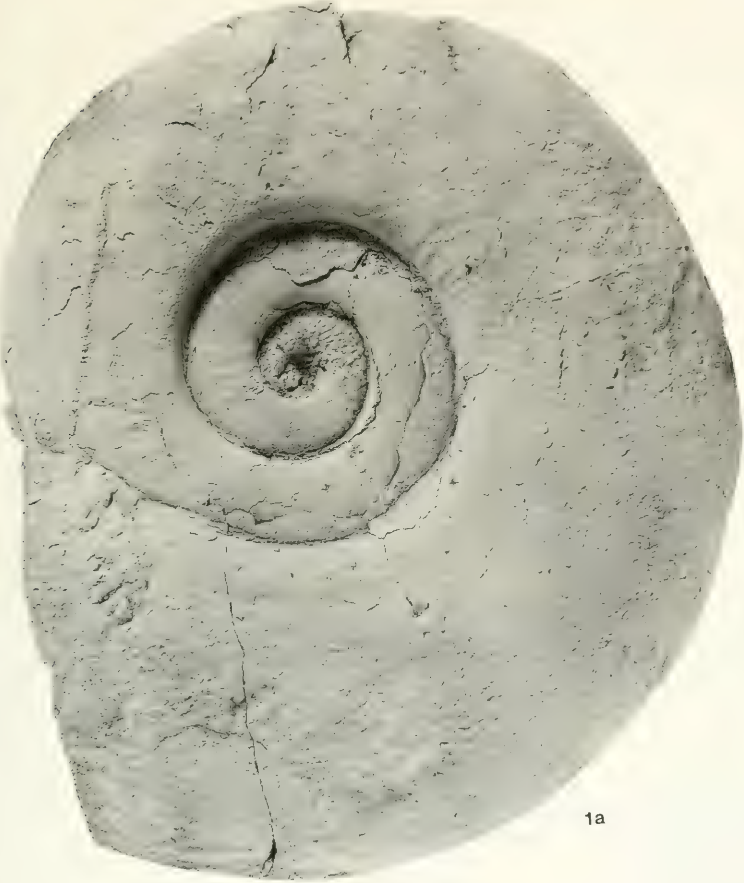
10a,b. Hypotype: GSC 98676; Locality: ET5 (GSC Loc. C-117003); Fannin Formation, Carlottense Zone.

11a,b. Hypotype: GSC 87806; Locality: ET5 (GSC Loc. C-117003); Fannin Formation, Carlottense Zone.

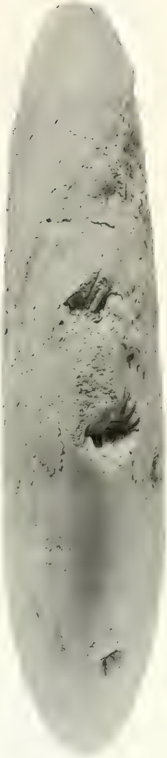
EXPLANATION OF PLATE 29

Figure is natural size.

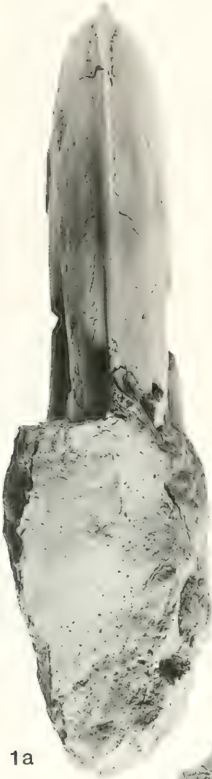
Figure	Page
1. *Lioceratoides* (*Pacificeras*) *propinquum* (Whiteaves, 1884).	71
1a,b. Plesiotype of McLearn (1932): GSC 6490; Locality: DT2 (GSC Loc. C-117033); Fannin Formation, Carlottense Zone or Lower Toarcian.	



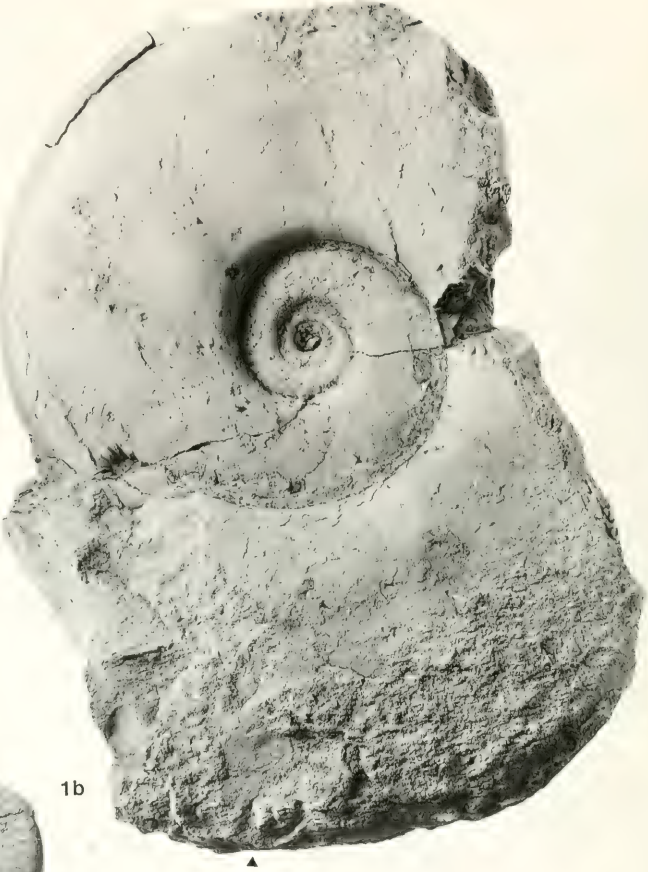
1a



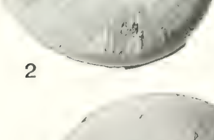
1b



1a

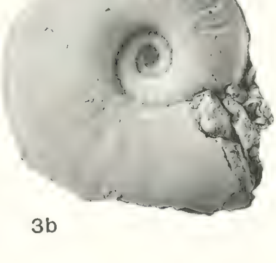


1b

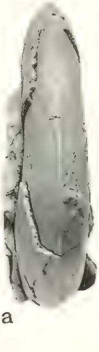


2

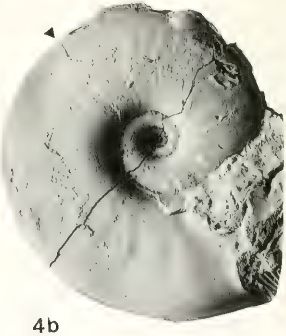
3a



3b



4a



4b

Explanation of Plate 30

All figures are natural size. The last suture is marked by an arrowhead.

Figure Page
1–4. *Tiltoniceras antiquum* (Wright, 1882). 72
  1a,b. Hypotype: GSC 98728; Locality: E62 (GSC Loc. C-81716); Fannin Formation, Carlottense Zone.
  2. Hypotype: GSC 98713; Locality E65 (GSC Loc. C-90544); Fannin Formation, Carlottense Zone.
  3a,b. Hypotype: GSC 98730; Locality: ET5 (GSC Loc. C-117002); Fannin Formation, Carlottense Zone.
  4a,b. Hypotype: GSC 98731; Locality: ET5 (GSC Loc. C-117003); Fannin Formation, Carlottense Zone.

INDEX

Note: Page numbers are in light face; plate numbers are in **bold face** type; Tf. indicates Text-figure.

Abbreviations 12, 18
Acanthopleuroceras Hyatt, 1900 35, 37
actaeon (d'Orbigny, 1844) 37
rursicosta Buckman, 1918 37, 40
stahli (Oppel, 1853) 36, 37
sutherlandbrowni Frebold, 1970 45
thomsoni, new species **7**,7,36,Tf.32
viligaensis Tuchkov, 1954 **20**, 51,Tf.36
whiteavesi Smith and Tipper, 1988 7, 36,37,Tf.26,32
accuratum, Leptaleoceras aff. **22**,57
actaeon, Tropidoceras **8**,36,37,Tf.32
Aegoceras aenigmaticum Gemmellaro, 1884 33
alloplocum Gemmellaro, 1884 34
sellae Gemmellaro, 884 42
taylori (J. de C. Sowerby, 1826) 41
aenigmaticum, Gemmellaroceras **6**,34,Tf.26
aequiondulatum, Protogrammoceras (*P.*) **24**,63,Tf. 38,39
Agassiceras centriglobum (Oppel, 1862) 23
Age of the Fannin Formation 12,13,15
Ghost Creek Formation 12,13
Rennell Junction Member 12,13
Sandilands Formation 12
Alaska 27,28,36,37,43,46,47,51,55,56,58,65,66
algovianum, Arieticeras aff. **20**,54
Algovianum Zone (Spain) 48
allifordense, Lioceratoides (*L.*) **26**,68,Tf.39
alloplocum, Gemmellaroceras cf. **10**,34,42
Allochthonous terranes 8,27,51
Amaltheus de Montfort, 1808 15,51,70
margaritatus de Montfort, 1808 51
cf. *nudus* (Quenstedt, 1856) 51
stokesi (Sowerby, 1818) **19**,**20**,51,Tf.36
viligaensis (Tuchkov, 1954) **20**,51,Tf.36
Amaltheus (*Nordamaltheus*) *brodnensis* Repin, 1974 52
(*Nordamaltheus*) *bulunensis* Repin, 1968 51
(*Nordamaltheus*) *viligaensis* (Tuchkov, 1954) 51
Ammonites actaeon d'Orbigny, 1844 37
algovianus Oppel, 1862 54
Bechei J.Sowerby, 1821 52
capillatus Denckmann, 1887 72
centriglobus Oppel, 1862 23
confusus Quenstedt, 1856 35
fieldingii Reynès, 1868 60
flandrini Dumortier, 1869 38
globosus Oppel, 1853 23
heterophyllus J. Sowerby, 1820 18
heterophyllus numismalis Quenstedt, 1845 20
kurrianus Oppel, 1862 64
laevigatus J. de C. Sowerby, 1827 24
lamellosus d'Orbigny, 1844 41
masseanum d'Orbigny, 1844 37
muticus d'Orbigny, 1844 43
natrix Schlotheim, 1820 35
nitescens Young and Bird, 1828 67
polymorphus quadratus Quenstedt 1845 35
ragazzonii Hauer, 1861 46,47
stokesi Sowerby, 1818 51
taylori Sowerby, 1826 40
valdani d'Orbigny, 1844 35,39
(*Harpoceras*) *domarensis* Meneghini, 1867 55
(*Harpoceras*) *mercati* Hauer var,*micrasterias* Meneghini 1874 56
(*Stephanoceras*) *crassus* Young and Bird var. *indunensis* Meneghini, 1885 49
(*Stephanoceras*) *mortilleti* Meneghini, 1875 49
("*Turrilites*") *valdani* d'Orbigny, 1842 35
angionus, Lioceratoides (*Pacificeras*) **27**,71,Tf.39
antiquum, Tiltoniceras **30**,70,72,Tf.39
Anisoloboceras Trueman, 1918 52
Apoderoceras cf. *A. subtriangulare* (Young and Bird) 45
Apoderoceras (*Miltoceras*) cf. *sellae* (Gemmellaro, 1884) 42
Arctic 27,66
Argentina 26,28,34,38,42,43,46,57
Argutarpites Buckman, 1923 63
Argutarpites argutus Buckman, 1923 64
Arieticeras Seguenza, 1885 15,54,59,61
Arieticeras aff. *algovianum* (Oppel, 1862) **20**, 54
apertum Monestier, 1934 54
compressum Monesier, 1934 57
disputabile (Fucini, 1908) **20**,**21**,54,Tf.37,38
aff. *domarense* (Meneghini, 1867) **20**, 55,Tf.37
cf. *domarense* (Meneghini) 57
gerardi Monestier, 1934 54,55
lupheri Imlay, 1968 **20**,54,55,Tf.37
cf. *micrasterias* (Meneghini, 1874) **20**,54,56
rimotum (Fucini, 1905) 56
cf. *ruthenense* (Reynès, 1868) **20**,56
simplex (Fucini, 1908) 56
Arthur (1985) 29
Ashcroft area, BC 29
Aveyroniceras Pinna and Levi-Setti, 1971 46
colubriforme (Bettoni, 1900) 46
italicum (Meneghini in Fucini, 1901) 47,50
striatum 48

Bassaniceras Fucini, 1929 63
bechei, Liparoceras (*Becheiceras*) **19**,**20**,52,Tf.36
Becheiceras Trueman, 1918 52
Becheoceras Dacqué, 1934 52
Bengston (1988) 15
Bettoni (1900) 19,20,23,41,46,47,55,64
Bettoniceras Wiedenmayer, 1977 46
Bettoniceras italicum (Fucini) 47
Blasco, Levy and Nullo (1978) 28,29
Blau and Meister (1991) 53
Blue Mountains (Oregon) 27
bodegae, Fanninoceras (*F.*) **2**,27
bonarellii, Phylloceras **1**,19,Tf. 25,26
Boreal faunas D8,51,52,72,73
Bouleiceras sp. 57
Bown (1991) 8
Braga (1983) 46,47,48,50,55,56,57,58,60,61,63,69
Braga, Comas-Rengifo, Goy and Rivas (1982) 34
Braga, Comas-Rengifo, Goy, and Rivas, (1985) 51,53,55
Braga, Jiminéz and Rivas, (1982) 58
Braga and Rivas (1985) 34,37,38
Bremer (1965) 33,35,37,38,40,41
Britain 40

Buckman, (1913) 72
Buckman (1914) 72
Buckman, (1918) 33,57
Buckman, (1920) 41
Buckman, (1922) 63,66
Buckman, (1923) 63
Buckman, (1927) 68

California 70
Callomon (1984) 13
Cameron and Tipper (1985) 7,9,11,12
Canavaria Gemmellaro, 1886 59
  cf. *C. morosa* of Imlay, 1968 59
  ? sp. **21**,59
Cantaluppi (1966) 47
Cantaluppi, (1970) 54,63,68
Cantaluppi (1972) 63
Cantaluppi and Brambilla, (1968) 47,58
Cantaluppi and Montanari, (1971) 46
Cantaluppi and Savi, (1968) 47,63,68
carlottense, Fanninoceras (F.) **2**,27,28,Tf. 30,31
Carlottense Zone 7,15,16,27,28,30,32,52, 55,59,60,64,66,67,68,69,70,71,72,73
Carter, Cameron and Smith (1988) 8
carteri, Fanninoceras (Charlotticeras) **5,6**,7,26,27,32,Tf.30
centriglobus, Cymbites **1**,23:Tf. 25,26
Cetonoceras Wiedenmayer, 1977 49
Chamosite 12
Charlotticeras, new subgenus 7,26,32
Chile 26,28,31,41,42,43,53,65
Coeloceras colubriforme Bettoni, 1900 46
  incertum Fucini, 1905 49
  italicum Meneghini in Fucini, 1901a 47
  mastodon Fucini, 1935 41
  mortilleti Meneghini, 1875 49
  Ragazzonii Hauer, 1861 47
  sub-anguinum Meneghini 47
Cólera, Rivas, Sequeiros, and Valenzuela, 1978 43,44,46
colubriforme, Reynesoceras **17**,46,47,48,Tf.35
colubriforme, Reynesoceras aff. **18**,47
confusus, Polymorphites **6**,35,Tf.32
compressum, Leptaleoceras **22**,57
compressum, Oistoceras **5**,7,53
Corvalan, 1962 55
crassum, Fanninoceras (F.) **4**,27,28,Tf.30
Crucilobiceras 43
  dolosum Wiedenmayer, 1977 49
  aff. *evolutum* (Fucini, 1924) 44
  mouterdei Frebold, 1970 44,45
  cf. *muticum* (d'Orbigny, 1844) 45
  pacificum Frebold, 1970 44
  cf. *submuticum* (Oppel) 43
Cumshewa Inlet Section 14,19,74
Cuvier (1797) 16
Cycloceras actaeon Futterer, 1893 37
Cymbites Neumayr, 1878 23
  centriglobus (Oppel, 1862) **1**,23,Tf. 25,26
  laevigatus (J. de C. Sowerby, 1827) **1**,24,Tf.25
  subcostulatus Spath, 1926 24

Dacqué (1934) 52
Dactylioceras 16,48,70
Dactylioceras? sp. 48
Dactylioceras cf. *kanense* 48
Dactylioceras helianthoides 48
Dactylioceratidae Hyatt, 1867 44,46
Dagis (1971) 71,73
Dagis (1974) 72
Dagis (1976) 51,52
Davoei Zone 26,27,41,42,43,44,46,47,49,52,53,61
dawsoni, Oregonites? **20**,7,59
Dayiceras? sp. 42
Dayiceras dayiceroides (Mouterde) 42
Dean, Donovan, and Howarth (1961) 14,40
Del Campana (1900) 41,47
Denckmann (1887) 72
Denckmann (1893) 72
Deroceras evolutum Fucini, 1924 44
diornatum, Protogrammoceras (Matteiceras) cf. **23**,67,Tf.39
disputabile, Arieticeras **20,21**,54,Tf. 37,38
Distefania Fucini, 1931 57
domarense, Arieticeras aff. **20**,55,Tf.37
Dommergues (1978) 41
Dommergues, Ferretti, Géczy, and Mouterde (1983) 34,47,49,60
Dommergues and Meister (1990) 41,41
Dommergues, Meister, and Fauré (1985) 67
Dommergues and Mouterde, (1978) 37
Dommergues and Mouterde (1980) 67
Dommergues and Mouterde, (1981) 37
Dommergues and Mouterde (1982) 44
Dommergues, Mouterde, and Phelps (1984) 38
Dommergues, Mouterde, and Rivas (1984) 42
Donovan (1954) 72,73
Donovan (1957) 23,24
Donovan (1994) 16
Donovan and Forsey (1973) 26,33,52
Donovan and Howarth (1961) 51
Donovan, Callomon, and Howarth (1981) 26,68
Dubar and Mouterde (1978) 34,40,41,44,47,63
Dubariceras Dommergues, Mouterde, and Rivas, 1984 42,44
  dubari Dommergues, Mouterde, and Rivas, 1984 42
  freboldi Dommergues, Mouterde, and Rivas, 1984 **16**,15,42,53,Tf.33
  silviesi (Hertlein, 1925) **15**,15,43
Du Dresnay (1963) 42,44,46
Dumortier (1869) 38

Elmi, Atrops, and Mangold (1974) 47
Emaciaticeras 59
Emaciatum Zone (Spain) 59,69
*Eoamaltheus*DHFD26,32
Eoderoceras 43,45
Eofuciniceras Cantaluppi, 1970 61
Eoprotogrammoceras Cantaluppi, 1970 63
Erben (1954) 57
Eerythraeum, Tropidoceras cf. **10**,38
evolutum, Metaderoceras **16,18**,44,45,Tf. 33,34

Fannin Formation 7,11,24,28,31,32,45,46,47,48, 50,55,56,57,58,59,61,63,64,66,68,69,72,73
fannini, Fanninoceras (F.) **3,5**,24,25,27,29,43,Tf. 27,30,31
Fanninoceras McLearn, 1930 7,15,70
  (Charlotticeras) carteri, new species **5,6**,7,26,27,32,Tf.30
  (Charlotticeras) maudense, new species **6**,7,26,27,32,Tf.30
  (Fanninoceras) bodegae McLearn, 1932 **2**,27
  (Fanninoceras) carlottense McLearn, 1930 **2**,27,28,Tf. 30,31
  (Fanninoceras) crassum McLearn, 1932 **4**, 27,28,Tf.30

  (*Fanninoceras*) *fannini* McLearn, 1930 **3**,**5**,24,25,27,29,43,Tf. 27,30,31
  (*Fanninoceras*) *kunae* McLearn, 1930 **4**,27,30,31,32,Tf.30
  (*Fanninoceras*) *latum* McLearn, 1930 **4**,27,31,32,Tf.30
  (*Fanninoceras*) spp. **4**,31,32
  disciforme Hillebrandt, 1981 27,28
  behrendseni (Jaworski) 27
  dolmagii McLearn, 1932 **3**,27,29
  lowrii McLearn, 1930 **4**,27,30
  oxyconum Hillebrandt, 1981 28
Fantini Sestini (1962) 55,56
Fantini Sestini (1974) 20
Fantini Sestini (1975) 46,47
Fantini Sestini (1977) 54,55,56,58
Fantini Sestini, (1978) 40,41
Fernie Group 27
Ferretti (1972) 56,63
Fieldingia Cantaluppi, 1970 60
fieldingii, Fieldingiceras **20**,**21**,60,Tf.37
Fieldingiceras Wiedenmayer, 1980 60
  fieldingii (Reynès, 1868) **20**,**21**,60,Tf.37
  morganense (Imlay, 1968) 60
  pseudofieldingii (Fucini, 1904) **21**,**20**,60,Tf. 37,38
Fischer (1971) 46,47,49
Fischer (1975) 57,65
flandrini, Tropidoceras **8**,**9**,38
Fontanelliceras, Fucini, 1931 58,59
  cf. *fontanellense* (Gemmellaro, 1886) 58
  juliae Fucini, 1931 58
  sp. **22**,58
France 38,39,44,49,53,55,57,58,60,61,67
Frebold (1964a) 32,51,53,54,56,57,60,72
Frebold (1964b) 28,29,68,71
Frebold (1966) 51
Frebold (1967) 26,28,29,30
Frebold (1970) 7,33,35,36,37,41,42,43,44,45,47,51,54,64,65,66
Frebold (1975) 51
Frebold and Little, (1962) 42
Frebold, Mountjoy and Tempelman-Kluit (1967) 51
freboldi, Dubariceras **16**,15,42,53,Tf.33
Freboldi Zone 7,34,35,42,43,46,47,49,50,53
Frontier Geoscience Program 7
Fucini (1896) 38
Fucini (1899) 23
Fucini (1900) 19,23,38,61
Fucini (1901a) 47,49,60,63,68
Fucini (1901b) 19
Fucini (1904) 60,61
Fucini (1905) 46,47,49
Fucini (1908a) 47,56
Fucini (1908b) 54,63
Fucini (1924) 44,63
Fucini (1929) 63
Fucini (1931) 54,56,57,58,68,71
Fucini (1935) 41,42
Fuciniceras Haas, 1913 61
  cf. *capellinii* of Imlay, 1968 59
  compressum (Monestier) 57
  cf. *inclytum* of Imlay, 1968 59
  aff. *intumescens* (Fucini, 1901) **22**,63,Tf.39
  lavinianum (Fucini) 63
  sp. **21**,63
  sp.A of Imlay, 1968 59
  sp.B of Imlay, 1968 59
  cf. *targionii* (Fucini, 1905) **22**,61
Futterer (1893) 37,38

Géczy (1959) 40
Géczy (1967) 51
Géczy (1976) 33,38,40,47,49,52,53,61
Geczya Fantini Sestini, 1977 54
Gemmellaro (1884) 19,34,38,42
Gemmellaro (1886) 59,63
Gemmellaroceras Hyatt, 1900 33,37,40
  aenigmaticum (Gemmellaro, 1884) **6**,34,Tf.26
  cf. *alloplocum* (Gemmellaro, 1884) **10**,34,42
  sp. **6**,34
Genus and species indet. **23**,67,Tf.38
Germany 35,38,39,40,58,72
Getty (1970) 35
Ghost Creek Formation 7,11,34,35,36,37,39,40,41,43,44,46
Gleviceras Buckman, 1918 33
  glevense Buckman, 1918 33
  ? sp. **2**,32
Glevumites Buckman, 1918 33
Graham Island 8,22,49,76
grahami, Reynesocoeloceras **12**,7,49
Grammoceras aequiondulatum Bettoni,Del Campana, 1900 63
  bassanii Fucini, 1901a 63
  Fieldingii (Reynès) 60
  penenudum Monestier, 1934 61
  pseudofieldingii (Fucini),Monestier, 1934 61
  sygma Monestier (1934) 60
Grammoceratoides Mattei, 1967 60
Great Britain 72
grecoi, Lioceratoides (*L.*) cf. **27**,68
Guex (1973) 58,68,70,71
Guibaliceras Buckman, 1918 33

Haas (1913) 61
Haida Gwaii 7
Hall and Howarth (1983) 66
Hall Formation (British Columbia) 34,42
Hallam (1965) 55
Hallam and Bradshaw (1979) 12
Harpoceras (*Dumortieria*) *haugi* Gemmellaro, 1886 59
  acutum (Tate),Wright, 1884 72
  aequiondulatum Bettoni, 1900 63
  allifordense McLearn, 1930 **26**,68
  antiquum Wright, 1882 72
  densecapillatum Fucini, 1924 64
  erythraeum Gemmellaro, 1884 38
  cf. *exaratum* (Young and Bird). Frebold, 1964a 64,66
  ? *Fieldingii* Reynès (1868) 60
  fontanellense Gemmellaro, 1886 58
  lavinianum Meneghini in Fucini, 1900 61
  maurelli McLearn, 1930 **26**,69
  percostatum Fucini, 1908b 63
  propinquum (Whiteaves). McLearn, 1930 **28**,**29**,71
  ? *pseudofieldingii* Fucini, 1904 60
  schroederi Denckmann, 1893 72
  sp. A. McLearn, 1932 **26**,69
  volubile (Fucini). Monestier, 1934 67
Hauer (1861) 41,46,47,48
Haug (1885) 37
Haug (1887) 33
Hector collection 40
Hemiparinodiceras Géczy, 1959 40

Hertlein (1925) 43
Hildoceras (*Arieticeras*) *domarense* (Meneghini, 1867) 55
  disputabile Fucini, 1908b 54
  intumescens Fucini, 1901a 63
  micrasterias (Meneghini) of Fucini, 1908a 56
  rimotum Fucini, 1905 56
  simplex Fucini, 1908b 56
  Targionii Fucini, 1905 61
Hillebrandt (1973a) 34,54
Hillebrandt (1973b) 57
Hillebrandt (1981) D26,28,29,30,31,34,41,42,43,45,46,50,54,56
Hillebrandt (1987) 26,30,35,38,42,45,65
Hillebrandt (1990a) 26,31
Hillebrandt (1990b) 42
Hillebrandt and Schmidt-Effing (1981) 26
Hillebrandt in Westermann (1992) 36,42,43
Hirano (1971) 47,51,58,68
Hirano (1973) 48,54
Hispanic Corridor 8
Hoffman (1968) 72
Hoffmann (1982) 35,53
Hoffmann and Martin (1960) 72
Howarth (1955) 59
Howarth (1957) 23
Howarth (1958) 51,53
Howarth (1973) 63
Howarth (1992) 65,66,67,70,72,73
Howarth and Donovan (1964) 21,23
Hungary 49,51,53
Hurwal Formation (Oregon) 37,43
Hyatt (1867) 37,52
Hyatt (1875) 24
Hyatt (1889) 23
Hyatt (1900) 33,34,35,20
Hydrocarbon potential 7

Iberian Peninsula 34
Ibex Zone 33,34,37,38,39,40,41,42,43,44,46,47,53,61,63
ICZN Opinion 996 (1973) 36
Imlay (1955) 51
Imlay (1968) 22,23,24,26,28,29,30,47,48,49,53,54,55,59,61,63,64,70
Imlay (1981) 26,28,30,36,42,43,44,45,47,51,53,54,56,57,58,64,65,66
imlayi, Pseudoskirroceras **13,14,15**,41
Imlayi Zone 7,14,20,34,35,38,40,41,42,43,44,46
incertum, Reynesocoeloceras cf. **12**,49
Indonesia 40,52
Indunoceras Wiedenmayer, 1977 49
  (*Bettoniceras*) *colubriforme* (Bettoni) 46
  (*Bettoniceras*) *mortilleti* (Meneghini) 50
Insular Belt 7,40
intumescens, Fuciniceras aff. **22**,63,Tf.39
involutum, Lioceratoides (*L.*) **26**,7,69,Tf.39
Isolated localities 22,76
italicum, Reynesoceras **18**,47
Italy 34,38,40,47,49,51,55,57,58,60,61,63,64,69,71

Jakobs, Smith, and Tipper, (1994a) 7
Jakobs, Smith, and Tipper, (1994b) 15,70
Jamesoni Zone 20,33,34,35,38,40,42,43,49,50,52,53
Japan 47,51,54,58,68
Jaworski (1931) 35

Keller Creek Formation (Oregon) 37
Krumbeck (1922) 40,52
kunae, Fanninoceras (F.) **4**, 27,30,31,32,Tf.30
Kunae Zone 7,15,20,22,23,24,27,28,29,30,31,32,33,43,45,47,48,49,50,51,53,54,55,56,57,58,59,61,63,67,68
Kunga Group 7,9,11
Kunga Island 7,8,12
Kunga Island Section 13,18,73
kurrianum, Protogrammoceras (P.) **24**,64,Tf.39

laevigatus, Cymbites **1**,24,Tf.25
Lange (1932) 50
latum, Fanninoceras (*F.*) **4**,27,31,32,Tf.30
Lehmann (1968) 72
Leioceras? *Grecoi* Fucini, 1901a 68
Leptaleoceras Buckman, 1918 57
  (*Fieldingia*) *pseudofieldingi* (Fucini) 61
  aff. *accuratum* (Fucini, 1931) **22**,57
  compressum (Monestier, 1934) **22**,57
  leptum Buckman, 1918 57
  macrum (Monestier, 1934) 58
  pseudoradians (Reynès) 57
  sp. **22**,56,58,Tf. 37,38
Leptonotoceras Spath, 1925 33
Levi (1896) 38,54
Lewis and Ross (1991) 9
Lioceratoides Spath, 1919 7,15,16,68,72
  (*Lioceratoides*) *allifordense* (McLearn, 1930) **26**,68,Tf.39
  (*Lioceratoides*) cf. *grecoi* (Fucini, 1901a) **27**,68
  (*Lioceratoides*) *involutum*, new species **26**,7,69,Tf.39
  (*Lioceratoides*) *maurelli* (McLearn, 1930) **26**,69
  (*Lioceratoides*) *naumachensis* (Fucini, 1929) 69
  (*Lioceratoides*) *serotinum* (Bettoni, 1900) 52
  (*Lioceratoides*) sp. juv. **26**,69,Tf.39
  (*Pacificeras*) *angionus* (Fucini, 1931) **27**,71,Tf.39
  (*Pacificeras*) *propinquum* (Whiteaves, 1884) **28,29**,71,Tf. 38,39
Liparoceras Hyatt, 1867 52
  (*Becheiceras*) *bechei* (J.Sowerby, 1821) **19,20**,52,Tf.36
  rotticum Krumbeck, 1922 52
Lithostratigraphy 12
Locality numbering system 14
Louise Island 8
Louise Island Section 13,19,74
lupheri, Arieticeras **20**,54,55,Tf.37

Margaritatus Zone 24,40,41,46,47,48,49,50,51,52,53,54,55,56,57,58,60,61,65,66,67
masseanum rotunda, Tropidoceras **10**,39,Tf.32
Matsumoto and Ono (1947) 68
Mattei (1967) 60
Matteiceras Wiedenmayer, 1980 67
Maude Group 7,9,11
Maude Island 7,45,59,72
Maude Island Section 15,74, Fold out
maudense, Fanninoceras (*Charlotticeras*) **6**,7,26,27,32,Tf.30
maurelli, Lioceratoides (*L.*) **26**,69
McLearn (1930) 24,28,29,30,31,68,69
McLearn (1932) 7,28,29,69,70,72
Mediterranean area 19,55,56, 57,59,60,63
Meister (1986) 21,23,26,37,38,39,44,52,53,60,61
Meister (1989) 23,46,48,55,56,58,60,65,
Meneghini (1867) 55
Meneghini (1870) 55
Meneghini (1874) 56

Meneghini (1875) 49
Meneghini (1881) 49
Meneghinia Fucini, 1931 54
Meridianus Zone (South America) 43,44,46,26
Metacymbites Spath, 1923 23
  centriglobus (Oppel, 1862) 23
Metaderoceras, Spath, 1925 15,43
  evolutum (Fucini, 1924) **16**,**18**,44,45,Tf. 33,34
  mouterdei (Frebold, 1970) **19**,44,45
  ? aff. *mouterdei* (Frebold, 1970) **16**,**19**,44,45,Tf. 33,34
  sp. **17**,42,46,Tf.33
  talkeetnaense Thomson and Smith, 1992 **17**,45,Tf. 33,34
  venarense (Oppel) 44
Mexico 57
micrasterias, *Arieticeras* cf. **20**,54,56
Microfossils 8,12
Miltoceras, Wiedenmayer, 1980 41,42
  aff. *sellae* (Gemmellaro, 1884) **11**,42
Monestier (1934) 19,23,42,47,54,55,56,57,58,60,61
Montfort (1808) 15,51,70
Moresby Island 8
Morocco 34,47,58,64,71
mortilleti, *Reynesocoeloceras* **12**,49,Tf. 26,35
Mouterde (1967) 35
Mouterde (1970) 43,44
Mouterde and Dommergues (1978) 37
Mouterde, Dommergues, and Rocha (1983) 23,53
Mouterde and Rocha (1981) 60
mouterdei, *Metaderoceras* **19**,44,45
mouterdei, *Metaderoceras* ? aff. **16**,**19**,44,45,Tf. 33,34

Nagatoceras Matsumoto in Matsumoto and Ono, 1947 68
Naxeniceras Fucini, 1931 57
Neofuciniceras Cantaluppi, 1970 61
Neolioceratoides Cantaluppi, 1970 68
Neoprotogrammoceras Cantaluppi, 1970 63
Neumayr (1875) 60
Neumayr (1878) 23
Nevada 27,28,36,47,55
Nicely Formation (Oregon) 24,60,63
Nordamaltheus Repin, 1968 51,52
North American Pliensbachian ammonite zones 11,14
Northwest Europe 21,24,26,40,51,53,57,67,70
Northwest European standard ammonite zonation 8,11,14

Obtusum Zone 24
Oistoceras Buckman, 1911 53
  angulatum (Quenstedt) 53
  compressum, new species **5**,7,53
Open nomenclature 17
Oppel (1853) 23
Oppel (1862) 35,54,65
Orbigny (1844) 37,41
Oregon
  22,24,27,28,29,36,37,43,46,47,55,56,57,58,59,60,63,65,70
Oregonites Wiedenmayer, 1980 55,59
  imlayi Wiedenmayer, 1980 59
  ? *dawsoni*, new species **20**,7,59
Ovaticeras 71
Ovaticeras facetum Repin, 1966 72

Pacific faunas 8
Pacificeras Repin, 1970 7,70
Pálfy, McFarlane, Smith, and Tipper (1990) 9,11
Pálfy, Smith, and Tipper (1994) 7,11
Paltarpites Buckman, 1922 63
  paltus Buckman, 1922 66
  sp. indet. Sey and Kalacheva, 1980 66
Paltechioceras cf. *P. harbledownense* (Crickmay) 36
paltum, *Protogrammoceras* (*P.*) cf. **24**,66,Tf. 38,39
Parisch and Viale (1906) 46
Partschiceras? Imlay, 1968 20
Pathology 47
Pérez (1982) 28,29,30,31,52
Phricodoceras Hyatt, 1900 40
  lamellosum (d'Orbigny,1844) 41
  cf. *taylori* (J,de C,Sowerby, 1826) **15**,41
Phylloceras Suess, 1865 18
  bonarellii Bettoni, 1900 **1**,19,Tf. 25,26
  frondosum (Reynès) 20
  sp. **1**,20,Tf. 25,26
  sp. Thomson and Smith, 1992 20
  waehneri (Gemmellaro) 20
  zetes d'Orbigny,Fucini, 1900 19
Phyllolobites Vadász, 1907 20
Pia (1913) 19
Pia (1914) 33
Pinna (1966) 46
Pinna and Levi-Setti, (1971) 46,47,50
Platyharpites Buckman, 1927 68
Pliensbachian-Toarcian transition 15
Polymorphites Haug, 1887 35
  confusus (Quenstedt, 1856) **6**,35,Tf.32
Polyplectus kurrianus (Oppel),Monestier, 1934 64
Portugal 35,44,53,67
Poulton, 1991 51,73
Praeleioceras Fucini, 1929 68
Praeleioceras pseudofieldingii (Fucini) 61
Praelioceras angionum Fucini, 1931 71
Proamaltheus Lange, 1932 51
Prodactylioceras cf. *colubriforme* (Bettoni) 46
  cf. *P. italicum* (Meneghini) 47
  cf. *P. mortilleti* (Meneghini) 49
propinquum, *Lioceratoides* (*Pacificeras*) **28**,**29**,71,Tf. 38,39
Protoarieticeras, Cantaluppi, 1970 54
Protogrammoceras Spath, 1913 15,16,61,63,70
  (*Matteiceras*) cf. *diornatum* Dommergues et al., 1985
    23,67,Tf.39
  (*Protogrammoceras*) *aequiondulatum* (Bettoni, 1900)
    24,63,Tf. 38, 39
  (*Protogrammoceras*) *kurrianum* (Oppel, 1862) **24**,64,Tf.39
  (*Protogrammoceras*) cf. *paltum* (Buckman, 1922)
    24,66,Tf. 38,39
  (*Protogrammoceras*) *skidegatense*, new species
    25,7,52,66,Tf. 38,39
  (*Protogrammoceras*)? sp. **23**,64,Tf. 38,39
  celebratum 64
  grisseli (Fucini). Dommergues and Mouterde, 1900 67
  pectinatum (Meneghini, 1881) 64
  cf. *serotinum*, in Sey and Kalacheva, 1980 68
Pseudoarieticeras Cantaluppi, 1970 54
pseudofieldingii, *Fieldingiceras* **21**,**22**,60,Tf. 37,38
Pseudoskirroceras Wiedenmayer, 1980 41
  imlayi Smith and Tipper, 1988 **13**,**14**,**15**,41

Quenstedt (1849) 35
Quenstedt (1856) 23,35,41

Quenstedt (1862) 23
Quenstedt (1883) 64
Quenstedt (1885) 23,39
Quinzio (1987) 28

Radstockiceras Buckman, 1918 26
Radstockiceras gemmellaroi 26
ragazzonii, Reynesoceras **18**,47,Tf.35
Raricostatum Zone 40,41
Regression 12
Rennell Junction Member 11,33,35,36,37,39,40,43,44,47,49,51
Rennell Junction Section 16,21,76
Repin (1966) 72
Repin (1968) 51,71,72
Repin (1970) 70
Repin (1974) 51,52
Repository 18
Reynès (1868) 47,56
Reynesoceras Spath, 1936 15,46,49
  acanthoides (Reynès, 1868) 47
  cf. *aegrum* (Fucini) 48
  colubriforme (Bettoni, 1900) **17**,46,47,48,Tf.35
  aff. *colubriforme* (Bettoni, 1900) **18**,47
  aff. *fallax* (Fucini) 46
  indunense 48
  italicum (Fucini, 1901) **18**,47
  mortilleti (Meneghini, 1875) 50
  ragazzonii (Hauer, 1861) **18**,47,Tf.35
  cf. *ragazzonii* (Hauer, 1861) 48
  sp. **18**,48
  ? sp. **18**,48
Reynesocoeloceras Géczy, 1976 49
  (*Bettoniceras*) cf. *colubriforme* (Bettoni) 46
  (*Bettoniceras*) cf. *mortilleti* (Meneghini, 1875) 50
  grahami, new species **12**,7,49
  cf. *incertum* (Fucini, 1905) **12**,49
  mortilleti (Meneghini, 1875) **12**,49,Tf. 26,35
  spp. **11**,50
Riccardi (1984) 42
Richardson (1873) 7
Ripariocerass Schindewolf, 1962 33
Rivas (1983) 43,44
Road 19 Quarry Section 15,20,75
Roman (1938) 35
Rosenberg (1909) 42
Rossland area (British Columbia) 42
rotunda, Tropidoceras masseanum **10**,39,Tf.32
rursicosta, Tropidoceras aff. **8**,39
Russia 51,52,54,67,68,70,72
ruthenense, Arieticeras cf. **20**,56

Sandilands Formation 7,9,11,37,39
Schindewolf (1961) 23,24
Schindewolf (1962) 33
Schlatter (1980) 37,38,39
Schlegelmilch (1976) 23,24,35,51,65,73
Schloenbachia propinqua Whiteaves, 1884 **28**,70,71
Schlotheim (1820) 35
Schröder (1927) 47,52,54
Section A 13,18,73
Section B 13,19,74
Section C 14,19,74
Section D 14,19,74
Section E 15,74, Fold out
Section F 15,20,75
Section G 16,21,76
Section H 16,21,76
Seguenziceras Levi, 1896 54
Seguentia Fucini, 1931 57
Seguenza (1885) 54
sellae, Miltoceras aff. **11**,42
Sey and Kalacheva (1980) 51,52,54,67
Shimer and Schrock, 1944 71
Siberia 72
Sicily 34
silviesi, Dubariceras **15**,15,43
Simpson (1855) 53
Sinemurian 9,19,33,41,49
Sinemurian-Pliensbachian boundary 14
Skidegate Inlet 66
skidegatensis, Protogrammoceras (*P.*) **25**,7,52,66,Tf.38,39
Smith (1981) 29,36
Smith (1983) 42
Smith (1986) 18,26
Smith (1988) 8
Smith, Beyers, Carter, Jakobs, Pálfy, Pessagno, and Tipper (1994) 7,8
Smith and Tipper (1986) 8,26,27,46
Smith and Tipper, (1988) 43,45
Smith, Tipper and Pálfy (1990) 11
Smith, Tipper, Taylor, and Guex (1988) 7,12,14,26,28,30,36,38,41,42,43,44,45,46,52,53,55,57,63,64,70,71
Smith and Westermann (1990) 8
Sonomia 27
South America 26,27,30,32,56,66
South Bay 72
Sowerby (1826) 41
Sowerby (1827) 24
Spain 38,46,48,49,53,55,57,58,59,60,61,64,69
Spath (1913) 61,63
Spath (1919) 3,68
Spath (1922) 40
Spath (1923) 23
Spath (1925) 43
Spath (1926) 24
Spath (1928) 37
Spath (1929) 33
Spath (1936) 46
Spath (1938) 23,40,52,53
Spatsizi area (British Columbia) 57
Sphenodiscus maudensis Whiteaves, 1884 33
Sphenodiscus requienianus? d'Orbigny,Whiteaves, 1884 **2**,28
Spinatum Zone 20,27,49,51,52,54,57,59,65,69
Standard zones 13
stokesi, Amaltheus **19**,**20**,51,Tf.36
Suess (1865) 18
Sutherland Brown (1968) 7
Switzerland 56,57,58,60,61,67

Taffertia 16
talkeetnaense, Metaderoceras 17,45,Tf.33,34
Talus collections 14
targionii, Fuciniceras cf. **22**, 61
Taseko Lakes area (British Columbia) 43
Tauromeniceras 59
taylori, Phricodoceras cf. **15**,41
Telegraph Creek area (British Columbia) 60

Tethyan faunas 8,20,21,34,38,41,42,44, 46,47,48,49,50,54,57,58,61,63,64,67,68,69,70
Thompson, Haggart, and Lewis (1991) 9
Thomson and Smith (1992) 26,31,35,36,38,42,43,44, 45,49,53,54,56,57,59,65,70,71,73
Tiltoniceras Buckman, 1913 15,16,70,72
  acutum Tate 72
  antiquum (Wright, 1882) **30**,70,72,Tf.39
  capillatum (Denckmann) 72
  costatum Buckman, 1913 72
  schroederi (Denckmann) 72
Tipper (1984) 42
Tipper, Smith, Cameron, Carter, Jakobs, and Johns (1991) 8,11,70
Toarcian 7,48,58,63,66,68,69,70,71,72,73
Tragophylloceras Hyatt, 1900 20
  loscombi 22
  new species? **1**,21
  sp. 21,28
  undulatum 22
Trinacrioceras Fucini, 1931 57
Tropidoceras Hyatt, 1867 37
  actaeon (d'Orbigny, 1844) **8**,36,37,Tf.32
  erythraeum (Gemmellaro, 1884) 34
  cf. *erythraeum* (Gemmellaro, 1884) **10**,38
  flandrini densicosta (Futterer, 1893) 38
  flandrini flandrini (Dumortier, 1869) **9**,38
  flandrini obtusa (Futterer, 1893) **8**,**9**,38
  masseanum rotunda (Futterer, 1893) **10**,39,Tf.32
  new species one **8**,40,Tf.32
  new species two **10**,40
  aff. *rursicosta* (Buckman, 1918) **8**,39
  sp. one **11**,40
Trueman (1918) 52
Tubellites Buckman, 1924 33
Tuchkov (1954) 51,52
Tulsequah area (British Columbia) 32
Turkey 33,38
Turneri Zone 24
Tutchericeras Buckman, 1919 33

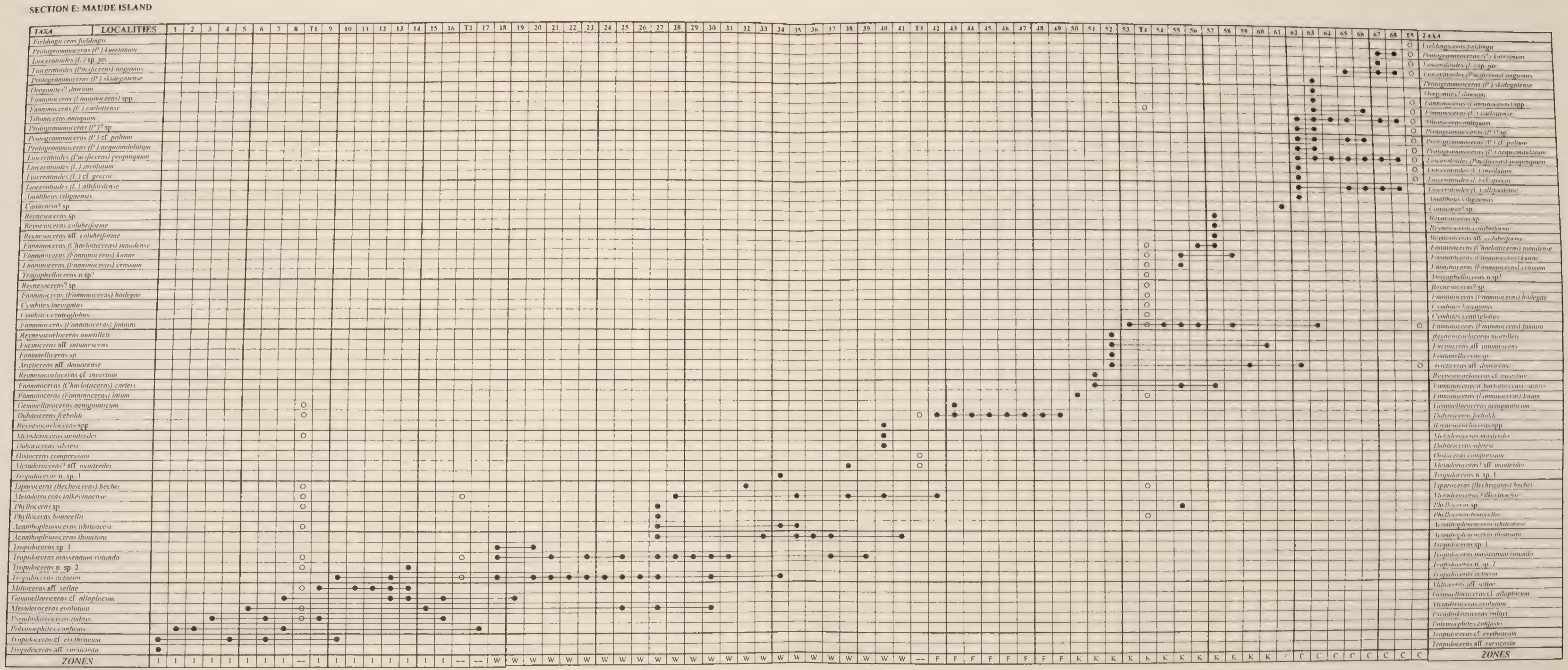
Ugdulenia Cantaluppi, 1970 57
University of British Columbia 8
Uptonia cf. *angusta* (Oppel) 42
  dayiceroides Mouterde 42
  cf. *ignota* (Simpson) 45
  cf. *obsoleta* (Simpson) 43
  silviesi Hertlein, 1925 43
Uptonia? sp. 53

Vadász (1907) 20
Vancouver Island 40
Vecchia (1949) 58
Vellutini and Bustin (1991a) 7
Vellutini and Bustin (1992b) 7
Venzo (1952) 63
viligaensis, Amaltheus **20**,51,Tf.36
Victoriceras Buckman, 1918 33
Vladivostok 52,68

Wallowa Mountains (Oregon) 27,29
Well Core (Section H) 16,21,76
Westermann (1992) 36,42,43
Whiteaves (1884) 7,40,71
Whiteaves (1900) 71
Whiteaves Bay 7,12,13,72
Whiteaves Bay Section 14,19,74
whiteavesi, Acanthopleuroceras 7,36,37,Tf.26,32
Whiteavesi Zone 7,15,20,33,34,36,37,38,39,40,42,43,44,45,46,51,53
Wiedenmayer (1977) 19,20,26,37,38,41,44,46,47,50,52,54,55,56,57,61
Wiedenmayer (1980) 37,41,42,47,48,51,55,56,57,59,60,61,63,67,68,70
Woodsworth (1991) 7
Wrangellia 7,8,51
Wright (1880) 41
Wright (1882) 72,73
Wright (1884) 72
Wrightia Gemmellaro, 1886 63

Yakoun Group 9
Young and Bird (1820) 45,49,64,66,67,73
Yukon 47

Zetoceras bonarellii (Bettoni) 19
Zieten (1830) 35
Zittel (1884) 18



Text-figure 20.—The ammonite fauna and biostratigraphy of section E. See Text-figure 11 for stratigraphic details and Text-figure 6 for the legend.

PREPARATION OF MANUSCRIPTS

Bulletins of American Paleontology usually comprises two or more separate papers in two volumes each year. The series is a publication outlet for significant, longer paleontological monographs (*i.e.*, more than approximately 50 printed pages), for which high quality photographic illustrations and the large quarto format are required.

Submissions are welcome from any author, regardless of institutional or organizational affiliation. Authors must, however, be members of the Paleontological Research Institution at time of publication; annual membership is currently US$25.00. Publication costs of the *Bulletins* are heavily subsidized by the Institution, but authors are currently required to pay illustration charges at a rate of $120.00 per plate and $35.00 per text-figure.

Important references for style and format are 1) *Bulletins of American Paleontology* "Instructions for Authors" (volume 108, number 347, pages 149–153); 2) *Chicago Manual of Style* (fourteenth edition) 1993. Recent issues of the *Bulletins* provide useful guides but note changes with the "Instructions for Authors" mentioned above.

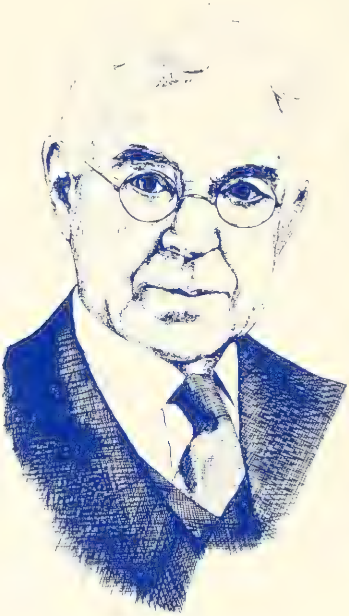
Manuscripts must be typewritten, and double-spaced *throughout* (including direct quotations, tables and references). All manuscripts should contain a table of contents, lists of text-figures and/or tables, and a short, informative abstract that includes names of all new taxa. Format should follow that of recent numbers in the series. All measurements must be given in the metric system, alone or in addition to their English system equivalents. The maximum dimensions for photographic plates are 178 mm × 229 mm (7 inches × 9 inches; outlined on this page). Single-page text-figures should be drafted for reproduction as single column (82 mm; 3¼ inches) or full page (178 mm; 7 inches) width, but arrangements can be made to publish text-figures that must be larger.

Authors must provide three (3) printed copies of the text and accompanying illustrative material. Authors are *strongly* encouraged to prepare their manuscripts on word processors, as this considerably expedites publication. On initial submission, however, only printed copies of the manuscript should be sent; the disk copy should be retained so that revisions can be made after the review process. The text and line-drawings may be reproduced xerographically, but glossy prints at publication size must be supplied for all half-tone illustrations and photographic plates. These prints should be identified clearly on the back.

Referenced publication titles *must be spelled out in their entirety*. Particular care should be given to reference format. Consult the "Instructions for Authors," referred to above, as several changes have been introduced with that issue. Citations of illustrations within the text bear initial capitals (*e.g.*, Plate, Text-figure), but citations of illustrations in other works appear in lower-case letters (*e.g.*, plate, text-figure).

Format of systematic descriptions should follow that in any recent number of the *Bulletins.*

Original plate photomounts should have oversize cardboard backing and strong tracing paper overlays. These photomounts should be retained by the author until the manuscript has been formally accepted for publication. The approximate position of each text-figure in the text should be indicated. Explanations of plates and text-figures should follow the References Cited.



Gilbert Dennison Harris
(1864 - 1952)

Founder of the *Bulletins of American Paleontology* (1895)

ISBN 0-87710-439-5

HECKMAN
BINDERY INC.
JULY 99
Bound-To-Please® N. MANCHESTER

SMITHSONIAN INSTITUTION LIBRARIES
3 9088 01358 5245